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HOMOLOGY, ANALOGY AND PLASIS

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IN THE days of Spallanzani and of John Hunter comparative anatomists did not scruple to employ experimental means as an aid to investigation. In their time no hard and fast distinction had been made between questions pertaining to structure and questions pertaining to function. Function and structure being viewed as more or less of a unity, biologists felt free to employ any available means in the investigation of their multifarious problems. In the process of historical development physiology hived off from anatomy and very soon two distinct sciences, each employing its own special technique and animated by its own particular aims, had replaced the more generalised biology of Hunter. During the nineteenth century the separation between them became profound. Of recent years we have witnessed a strong tendency on the part of zoologists and anatomists to recur to the experimental method. It began with Darwin and to a less degree with Milne Edwards. It received a very strong impulse in a special direction from Wilhelm Roux and in another direction from Gregor Mendel. More particularly in America, where a strong group of men, prepared in Johns Hopkins University by the joint labors of Brooks and of Newell Martin, were ready at an opportune moment to develop and greatly to extend the biology of Roux and of Mendel, zoology is now viewed as an experimental rather than as a comparative science. In process of time no doubt matters will readjust themselves and the comparative method of studying structure will again come more into vogue. When it does it too will have to be handled experimentally.

As physiologists are not generally aware of the opportunity open to them of participating in some of the classical problems of comparative anatomy, and as the morphology of our fathers has for the moment fallen on evil days, it seemed worth while to go over the history of the original separation between physiology and comparative anatomy with a view to make some constructive attempt towards a *rapprochement* between them. The whole issue is rather a wide one and cannot well

be covered in a short article, but the matter may be partially handled by discussing afresh the vexed question of homology and analogy. The line of treatment here presented, of necessity somewhat formal, owes its origin to a suggestive communication by Keith Lucas on *The Evolution of Animal Function*—cf. also E. S. Russell (1916) and Tait (1917,a). Lucas correctly traced the ultimate complete separation between physiology and comparative anatomy to the outcome of the famous discussion that arose between Cuvier and Geoffroy St. Hilaire as to the criteria of comparison of animals for purposes of classification. In this discussion, as we know, Geoffroy prevailed over Cuvier.

HOMOLOGY AND ANALOGY

Let us go back to the time of Cuvier and Geoffroy. Many of the characteristic parts of animals, head, eyes, legs, wings, etc., had long received at the hands of mankind distinctive names indicating equivalence or correspondence. A child can scarcely fail to recognize the essential similarity between, say, the legs of a fly and the legs of a cat. The comparative anatomists, having recognized a certain number of different types or patterns of bodily structure, were now faced with a difficulty of a novel nature. An insect and a bird—to select a particular pair of animal forms—belong to two different types of organization. In what sense are the wings and the legs of the insect equivalent to those of the bird? The penetrating mind of Geoffroy St. Hilaire seized upon a way out of this difficulty. The wings of the insect resemble those of the bird only in so far as they subserve the same function. Though the bird, in virtue of its power of flight, may seem to occupy an anomalous position in the vertebrate series, in essential structure it thoroughly conforms to type, and comparison shows that the bird's wing is, from a structural point of view, the equivalent of the fore-limb of any other land vertebrate. The insect's wing, which is not a modified limb, is obviously a different article.

The conclusion was that, for a decision on questions pertaining to the arrangement or classification of animals, we should close our eyes to similarities dependent on mere equivalence of function, and concentrate solely upon intrinsic structural features. Owen later codified the terminology by which these two forms of resemblance are distinguished. Parts or organs of one animal which have the same function as parts or organs in a different animal he termed *analogous*. Parts or organs structurally identical under every variety of external form and of function he termed *homologous*. Biologists thereupon decided to discount analogies, the determination of homologies being considered as rendering better service for their purpose.

The introduction of this distinction between analogy and homology, valuable and indispensable as it was for its special purpose, reacted upon the outlook of physiologists and of anatomists alike. It appeared as if a verdict had been pronounced against the right of physiology to participate in the larger problems of structure, and the effect was to produce a disunion of effort between the two colleagues in what had previously been considered common, or at least closely contiguous, territory. Medical demands being urgent, the physiologists fell back almost entirely upon study of the mechanism of the human body, and it is curious to note how their science remained thereafter unresponsive to and untouched by some of the broader and more liberal developments of biological investigation,

developments with which comparative anatomy continued in complete rapport.

The adjective *homologous* is in reality a geometrical term and applies to corresponding members of similar figures. For example, in the two similar pentagons $\alpha\beta\gamma\delta\epsilon$ and *ABCDE* the line $\alpha\gamma$ is homologous with the line *AC*. So too are the sides $\alpha\beta$ and *AB*, $\beta\gamma$ and *BC*, $\gamma\delta$ and *CD*, respectively homologous. In "ideal" morphology the use of the word "homologous" in this positional sense is appropriate and serves a useful purpose. It condenses into one phrase Geoffroy St. Hilaire's famous *principle of connexions*, according to which parts are comparable when they occupy corresponding positions, i.e., have identical spatial relations, in the organisms selected for comparison.

Owen's definition of analogy is: "A part or organ in one animal which has the same function as another part or organ in a different animal." Now, in text-books of comparative anatomy we find that it is customary to analyze animals into systems of organs, thus:

Integumentary,
Skeletal,
Muscular,
Alimentary,
Excretory,
Circulatory,
Respiratory,
Nervous,
Sense Organs,
Reproductive,
Endocrine.

The original conception of this device is due to Cuvier, and it will be noted that the names of these systems, which recur almost en bloc in different phyla, are predominantly functional in signification. Systems, however, are made up of "parts or organs," and as modern comparative anatomists are only too well aware, the fact of analogical resemblance between organs is in itself a thing of extreme interest—cf. Willey. The exponents of ideal morphology discarded likenesses of analogy for two reasons: (1) they elected to believe that structure is prior to and determines function, or, as Geoffroy St. Hilaire put it, "animals have no habits but those that result from the structure of their organs; if the latter varies, there vary in the same manner all their springs of action, all their faculties and all their actions;" (2) equivalence in the matter of spatial relationships, being a more precise conception than "functional" equivalence, could be forthwith applied as a criterion of comparison.

THE QUESTION OF FUNCTIONAL EQUIVALENCE

Let us consider for a moment some of the complications involved in so-called functional equivalence.

The difficulty of precise definition. For simplicity let us begin with a concrete example. Let us take an obvious action, such as that of a wing, which is used for flying. How do we define flight? Flight involves in the first instance progression through the *air*, but so does a mere fall as well as a leap. We therefore incorporate as an essential element the idea of *support* by the air itself. So modified, the definition still includes the drifting of a balloon. We rectify once more and impose the condition that the flying body must be *heavier than air*. Soaring and parachuting have still to be eliminated. We amend again and stipulate that *the energy determining the progression must not be derived from movement of the air itself*. With it all we have yet failed to eliminate gliding, as from a precipice or other attained height. So we lay down the further condition that *the energy involved shall not necessarily have been imparted before launching into the air*. With these several stipulations we finally conclude that the flying body, itself heavier than air, must be a source of energy

and that this energy is used simultaneously for its support and for its forward progression, in virtue of the reaction or inertia of the air. So defined, flight would include the flight of a bird or of an insect, of a flying machine, of a rocket and of an aerial torpedo, but not of a flying fish, of a pterodactyl or of a flying phalanger. To one whose pursuits have lain chiefly in the field of comparative anatomy such analysis may appear fussy and beside the point, particularly in its invocation of energy considerations, and that to the exclusion of the wing itself. To the student of function this mode of procedure is a *sine qua non;* it is his comparative method; in which respect our cited case is merely an example of a general and invariable mode of attack. With advance of time, too, the elaboration of specification tends to increase, and even our example involves elements that are novel since the time of Cuvier and Geoffroy. Similar analysis is involved in terms like walking, running, swimming, breathing, feeding, excreting, etc. When we say that a system of organs, or even a particular part, subserves a certain use or function, it is necessary, in order to avoid confusion, to be scrupulously explicit. As a very simple illustration let one consider the fundamental difference between feeding of a Paramecium, which ingests food particles bodily into its protoplasm, and the corresponding process in higher animals, which first reduce their food to a soluble condition before absorption.

The two meanings of "function." Another, and more vital, complication is that the word function is ordinarily employed in two quite distinct senses: (1) to indicate the general *use* or application of an organ, as in the phrase "to subserve a function"—the cases already cited come under this category; (2) to cover the individual events or interior processes which go on in its constituent cells, i.e., the essential or intrinsic physiological mechanism of the part. Modern physiology has concerned itself particularly with function in the second sense, which we may here for convenience call "Function *B*," whereas Geoffroy St. Hilaire and Owen, in their institution of the conception of analogy, were thinking only of the first, which we may call by the name of "Function *A*." Thus it is that a physiologist of the present day, suddenly confronted with Owen's definition of homology and of analogy, is at a loss to understand from the examples cited by way of illustration wherein the averred distinction lies. He instinctively looks for a difference in essential mechanism, let us say, between legs, wings and fins, and finds none. To him all these appendages are simply pegs or bone-linkages moved in an adequately coördinated fashion by muscles under the domination of the central nervous system—cf. Keith Lucas.

Similar use but different intrinsic mechanism. On the other hand—and this involves a third complication—it has been found that organs which fulfil equivalent requirements so far as the needs of the animal are concerned, may differ in intrinsic physiological mechanism. Thus, the heart of a mammal and the heart of the king-crab *Limulus* perform in each case the office of pumping the blood. The muscle of the mammalian heart, however, exhibits a marked refractory phase after each beat, cannot be held in continued contraction by serial stimulation and has inherent rhythmic power, whereas the muscle of the heart of *Limulus* has no enduring refractory phase, can by a series of stimuli be maintained in steady contraction and ceases to beat when separated from the central nervous system (Carlson). To Geoffroy St. Hilaire and to Owen these hearts, which prove on

experimental investigation to be so dissimilar, would doubtless have appeared as functionally equivalent just because both subserve the same use.

As another example one might adduce those types of articulation which in certain animals permit not only of free hinge movement in various directions but also of torsional movements. In vertebrates these are the ball and socket joints. An articulation permitting similar freedom of movement is the coxo-basal articulation of isopods (Tait, 1917,b). The design of this joint is quite different from that of the bony ball and socket. The hollow cylinder of the basipodite rests by its edge upon a projecting hook-like process of the coxa. Another device designed to give similar results is that present in the Balanidae (Tait and Emmons). The operculum of these sessile cirripedes does not articulate at any fixed point directly with the surrounding shell. It rests upon a closed cushion of fluid, and is bent in any given direction or torsionally rotated by means of appropriate muscles, the underlying fluid being meantime subjected to high pressure. In these various articulations, therefore, we find three different types of physical or physiological mechanism, all designed to give the same complex result.

Indications are not wanting that equally striking differences in intrinsic mechanism exist between selected organs of one animal group and their accredited analogues in other groups.

By way of résumé we may note the following. In asserting a functional difference between organs, one must distinguish clearly between function in the sense of use (Function *A*), and function in the sense of intrinsic mechanism (Function *B*). In the historical separation of likeness by "analogy" from likeness by "homology," the use of a part (Function *A*) is what was meant by its function. It is particularly to be noted that neither Geoffroy St. Hilaire nor Owen established any case of homology in which function in the sense of intrinsic mechanism (Function *B*) varies; in all the subsequently accepted cases of homology suggested by them the essential mechanism remains unchanged. At the same time it is possible to point to deep-seated differences of function (i.e. Function *B*) in organs which they would undoubtedly have slumped together as analogous.

It is true that Geoffroy sought to develop a detailed homology between a skeletal segment of an arthropod and a vertebra of the Chordata. Von Baer, also on homological grounds, explained the conformation of a vertebrate as being a compound between articulate and molluscan elements, the animal parts (*sensu* Bichat) of the vertebrate being of the articulate type, the vegetative parts being of the molluscan type. These and many similar erroneous attempts at homological reasoning, perfectly valid according to Geoffroyian criteria, were seen to be grotesque so soon as the doctrine of likeness by descent became prevalent; but it may also be pointed out that such cases of fictitious homology would equally have broken down if tested by the criterion of function in the sense of intrinsic mechanism (Function *B*).

OWEN'S "ANALOGY" NOT A PURELY FUNCTIONAL CONCEPTION

In view of an occasional misconception it is well to bear in mind that though Owen's definition of analogy is phrased in purely functional terms, it nevertheless bears an inherent structural connotation. We might illustrate by reference to the so-called reticulo-endothelial system. When foreign particles are injected into the circulation of a mammal they come to

rest in three several organs, viz. the spleen, the liver and the bone marrow. Microscopic examination shows that in these sites the normal vascular endothelium is wanting, and that the particles have been ingested by special cells, the Kupffer cells of the liver, the cells of the splenic ellipsoids and other special cells of the marrow. Now, in accordance with the literal terms of Owen's definition it might be stated that these phagocytic vessel-lining cells, which all react in the same way towards particles, are "analogous" elements.

It should be kept in mind, however, that the original purpose of the definition of analogy was not to serve a physiological end, but to prevent confusion in a structural inquiry. The analogous organs of interest to Geoffroy St. Hilaire were, for example, the legs or arms of arthropods, of cephalopods and of vertebrates; the wings of insects, of birds and of bats; the valves of Cirripedia, of brachiopods and of acephalous molluscs; the tail-parts of arthropods and of vertebrates; the tentacles or antennae respectively of gastropod molluscs and of arthropods—in each case structures which to the laity might appear identical, but whose fundamental structural inequivalence is for the first time revealed by comparative anatomy. While Owen's definition of analogy was so phrased as not to include any formal reference to structure, the context sufficiently shows that it carried a structural connotation, being designed to anticipate the very blunder that on a superficial view might cause embarrassment. Introduced as a complementary term to homology, for use in purely structural inquiries, it was originally aimed at organs which in virtue of similar environment show an external structural correspondence. On its first introduction therefore the word analogy had no exclusively functional meaning, contrary to what some modern writers occasionally assume. Essentially it involved a structural connotation, and the real truth is that Geoffroy and Owen, in setting up analogy against homology, were struggling to formulate a distinction between what we should now prefer to call similarity by convergence and similarity by descent.

THE EMBRYOLOGICAL OR GENETIC CRITERION OF HOMOLOGY

With the advent of Darwinism a curious thing happened in regard to the criteria of homology. Structural likenesses being seen to depend, not on unity of plan, but on descent from common ancestors, the original geometrical conception of homology, which for the sake of distinctness we might now call "positional homology," was allowed quietly to lapse. One might suppose that the term homology, having outlived its *raison d'être*, would ultimately have died out. Instead, it adapted itself to its new surroundings and emerged in a new guise and with transformed meaning, which we shall here designate as "embryological homology." The change of meaning of the word, which we have indicated by prefixing to it special adjectives, occurred so easily and so naturally that for a time the matter escaped analytical inquiry.

Fritz Müller was early in the field with support for Darwin's theory of descent. Müller's main contention was that during the development of various animals, especially the Crustacea, the embryos pass through successive stages which resemble the presumable line of historical descent of the adults. Haeckel, seizing upon this conception, which he extended with a wealth of illustration to the animal kingdom at large, gave it concise form in his statement of the so-called "biogenetic

law," according to which the ontogenetic development exhibits an abbreviated repetition of phylogenetic history, in other words that individual embryonic stages represent reanimated but schematised ancestors of the fully developed animal. If now two apparently diverse organisms are found to be structurally comparable, part for part, in the adult stage, will not their individual homologies be rendered more evident by examination of their development (which, by hypothesis, mirrors their phylogeny) before specialisation or extreme differentiation has occurred? Particularly apposite evidence in support of this notion was already to hand from the science of embryology. Consequently we find Haeckel announcing that "true homology can only exist between two parts which have arisen from the same primitive 'Anlage' (embryonic representative) and have deviated from one another by differentiation only after the lapse of time."

For the moment the old positional or geometrical conception of homology had faded into the background. Gegenbaur's definition of special homology, viz., "the relationship between two organs which have had a common origin, and which, as a corollary, have arisen from the same Anlage," incorporates to the full the biogenetic law of Haeckel. The new interest attaching to the establishment of "homologies" was thus expressed by Gegenbaur: "Homology . . . . corresponds to the hypothetical genetic relationship. In the more or less clear homology, we have the expression of the more or less intimate degree of relationship. Blood-relationship becomes dubious exactly in proportion as the proof of homologies is uncertain."

How now does the amended criterion of homology work out in practice? For one thing the old bugbear of analogical resemblance or similarity by adaptation was not yet lightly to be exorcised, and we find Haeckel remarking: "In evaluation of anatomical resemblances . . . . everything in the last issue invariably depends on the decision whether the ultimate correspondences in structure are to be looked upon as homologies (maintained by common descent) or as analogies (acquired by similar adaptation). Important as it is, this very decision is often extremely difficult." Another perplexity inherent in the new definition was that which occurs to so many young students of morphology, namely, of fixing a limit of commencement to the "Anlage" of an adult organ; for a group of such "Anlagen" may have themselves a common "Anlage" in an earlier period of development; in this way one arrives at the blastomeres and finally at the ovum itself. Partly as a correction against this perfectly pertinent but perfectly useless extension of the embryological criterion—which, interpreted phylogenetically, would make almost all organs of any one phylum homologous one with another—and partly because of greater convenience in practice, the evolutionary morphologists, while introducing the embryological conception into their definition of homology, continued in the habit of establishing homologies by comparison of adults, just as the older anatomists did. It has ever proved more easy to alter a creed than to uproot long-established usages associated with an older faith. While the morphologists professed embryological homology, their conduct alternated between the homology that depends on simple position and that which is defined in terms of similarity of development.

If we inquire as to the place allotted to function in the new order of things, we find that it was consistently discussed in the sense of use or application (Function

A), just as of old. As an extreme illustration one might select Reichert's demonstration by embryological means of the homologies of the auditory ossicles of mammals, which proved to be a modification of the whole hinder portion of the lower jaw, as it exists in reptiles, as well as of the separate quadrate. The striking nature of this case leads Gaupp to remark: "Thus we have here in the history of the auditory ossicles of mammals a highly remarkable case of change of function, perhaps the most remarkable case in the whole realm of vertebrate morphology; skeletal parts which previously formed important members of the mandibular apparatus, are in the mammal alienated therefrom and assigned to an entirely new duty." In this particular instance, where a series of articulating bones commences and ends as a bone-linkage, it is almost unnecessary to point out that as a form of intrinsic physiological mechanism it remains almost the same. To this day the question has scarcely been raised whether identity in respect of Function *B* should not be incorporated as an essential element in our predication of likeness by homology.

HOMOGENY AND HOMOPLASY

As we have just seen, morphologists were not always careful to distinguish the homology based on comparison of adult characters from that which is embryologically determined. By injecting into positional homology all the implications of the theory of descent, they persuaded themselves that when they determined homologies after the old fashion, they were establishing embryological homology. In an important communication published in 1870 Ray Lankester drew attention to the danger of this procedure. In order to rectify matters he proposed at the same time a reform of the terminology, his statement being somewhat as follows:

He first suggested that organs may appropriately be called *homogenetic* if the common possessors are derived from ancestors that possessed the same organ. But homology had not infrequently been based upon considerations of pure position. Thus, the four cavities of the bird's heart had been said to be homologous with the four cavities of the mammalian heart, in spite of the fact that the common ancestors of mammals and birds had in all probability but three heart cavities, and in spite of the further fact that the right ventricle of a bird's heart does not develop in the same way as the right ventricle of a mammalian heart. Again, certain muscles in the limbs of Sauropsida were said to be homologous with other muscles in the limbs of Mammalia, although the presumption was that no such muscles were present in the limbs of the common amphibian ancestors. (Here Lankester was following Huxley's now discredited derivation of mammals from an amphibian and not from a reptilian stock.) "Again," says he, "it may perhaps be admitted that the common ancestors of the Osseous Fishes and Mammalia had a skull of decidedly undifferentiated character, with a much less amount of differentiation than is observed in the skulls of either of these groups. It is only in so far as they have parts represented in the common ancestor that we can trace *homogeny* in these groups; and yet the *homology* of a vast number of bones in the skull of the two is discussed and pointed out." He further instanced the serial homologies, in which a correspondence is traced in detail between the structures composing, say, the fore-limb and those composing the hind-limb of one of the higher vertebrates. His conclusion was that something over and above

simple *homogeny* is in such cases connected by the term homology, and he proceeded to state the proposition thus: "When identical or nearly similar forces, or environments, act on two or more parts of an organism which are exactly or nearly alike, the resulting modifications of the various parts will be exactly or nearly alike. Further, if, instead of similar parts in the same organism, we suppose the same forces to act on parts in two organisms, which parts are exactly or nearly alike and sometimes homogenetic, the resulting correspondences called forth in the several parts in the two organisms will be nearly or exactly alike. . . . . I propose to call this kind of agreement *homoplasis* or *homoplasy*. . . . . What is put forward here is this: that under the term 'homology', belonging to another philosophy, evolutionists have described and do describe two kinds of agreement—the one, now proposed to be called 'homogeny', depending simply on the inheritance of a common part; the other, proposed to be called 'homoplasy,' depending on a common action of evoking causes or moulding environments on such homogeneous parts, or on parts which for other reasons offer a likeness of material to begin with."

Lankester's paper is perhaps the most interesting *tour de force* in the history of the subject. We shall take up in order the questions it raises.

Homogeny. As already indicated, this is simply a distinctive name for embryological homology, so designed as to preclude any chance of misapplication or misapprehension. Because of its doubtful antecedents (note his phrase, "belonging to another philosophy"), he drops the word homology altogether.

Homoplasy. This conception, being a novel one, demands and obtains chief consideration in his paper. It has for us a two-fold interest: (1) in respect of the plasis or moulding idea; (2) in respect of the relation of homoplasy to the old analogy.

Plasis or moulding. Significant is his clear enunciation, at this early date, of the conception that (by whatever imaginable means) forces of environment act upon and mould developing structure. The language, be it observed, is not that of natural selection; actively determining or causal *forces* are predicated. Though the experimental procedure is lacking, his speech is essentially the speech of *Entwicklungsmechanik*, and to this extent foreshadows a new outlook.

Homoplasy and analogy. In view of what has preceded, we naturally ask: "In what regard, if any, does homoplasy differ from the old (structural) analogy?" Lankester did refer to the point in his paper, but elected, for reasons which he does not specify, to differentiate between the two. By confining the application of his term "homoplasy" to organisms or parts of organisms which are nearly or exactly alike, he seems deliberately to have limited its scope. Possibly, too, he was influenced by the feeling that the classical cases of analogy would presuppose forces of external environment, whereas in his illustrations of homoplasy the internal environment of the animal is apparently the main moulding influence.

In later life Lankester has shown a disposition to extend the scope of his homoplasy so as to cover all cases of convergence or parallelism. His original definition involved simultaneous specification of two separate likenesses, (1) "identical or nearly similar forces of environments," (2) "parts of an organism which are exactly or nearly alike," or "parts in two organisms, which parts are exactly or nearly alike," or "parts which for other reasons show a likeness of

material to begin with." For establishment of homoplasy, according to the definition, both conditions have to be satisfied. Condition (1) is phrased in sufficiently general terms to include external as well as internal environment. The main question that arises is the precise degree of restriction imposed by condition (2). In a reply to H. F. Osborn (1907) he says, "Can you imagine cases of convergence or parallelism which are not covered by the definition I gave of homoplasy? What organs are parallel in any two animals and yet have no likeness at all—even the most general—in their material?"

From these sentences it would appear that Lankester might have been willing to omit condition (2) from his definition. It must be kept in mind that in his original paper he did more than define homoplasy; he committed himself to a statement or proposition as to the action of similar environmental forces on two separate things, and, for the purpose of this proposition, condition (2) may have been necessary. When, however, close structural likeness is seen to arise between two very diverse things—likeness which is obviously correlated with, or rather dependent upon, identity of environment—it should be quite permissible to designate the resemblance as homoplasy. The various instances of analogy are just of this kind, e.g., the wings of bats, of birds and of insects; the eyes of Pecten, of cephalopods and of vertebrates; the otocysts of various invertebrates and their labyrinthine equivalents in vertebrates; the division of the body into leaves, stem and roots in the case of the higher plants (diploid generation) and of mosses (haploid generation); the hyphal form of parasites, such as the Fungi among lower plants, *Rafflesia* among higher plants, *Sacculina* among animals; the hold-fast organs (haptera) of seaweeds and green algae, perhaps the adhesive roots of ivy and adhesive stems of *Ampelopsis*, the adhesive base of certain unicellular animals (e.g., *Vorticella*), of sponges, of zoophytes, of sea anemones, of crinoids, of Cirripedia and of sessile tunicates. If this interpretation of Lankester's meaning be correct, then, as Osborn says in an amended statement, "Lankester's homoplasy is equivalent to analogous evolution, to parallelism, or convergence."

EXPERIMENTAL CONTRIBUTIONS TO HOMOPLASY

Just as Owen based the conception of analogy on morphological evidence, so it was by purely morphological testimony that Lankester was led to institute the idea of homoplasy. Of recent years physiology and experimental embryology have begun—in some cases almost unwittingly—to furnish evidence touching upon the question of homoplasy. With the help of some illustrative cases we may briefly indicate the significance of these experimental contributions to the subject.

Examples. It is well known that normal development of (1) the accessory sexual organs (e.g., the vagina, uterus, Fallopian tubes and mammary glands of the female, the vesiculae seminales and prostate gland of the male) and (2) of the so-called secondary sexual characters of mammals, is dependent upon the presence of the gonads. When the ovaries or the testes of a vertebrate are removed in youth, the growth and differentiation of the accessory sexual organs is faulty and the secondary sexual characters are absent. By grafting into the castrated animal a gonad taken from another animal of similar species and sex, the defective organs or characters are induced to resume development. Experiment has shown

that the effective part of the gonad, in the case of the male at least, is, not the spermatogenic tissue, but the interstitial cells or so-called "interstitial gland." Obviously the Anlage or embryonic representative of, say, the prostate gland of the young male animal does not of itself possess the power of developing to completion; for the attainment of full structural maturity a "hormone" derived from the interstitial gland is necessary.

In most cases of development no such correlation of separate parts (one primary, the other secondary) has as yet been verified. At an early and quite undifferentiated stage of development of the respective parts, Braus removed the little outgrowth or bud which represents the hind-limb of a tadpole and inserted upon the wound of the trunk thus caused the bud of a fore-limb. In its abnormal situation the latter grew and developed into a typical and full-sized fore-limb, in which not only the various bones, muscles, joints and ligaments were complete, but in which the orientation of the mature transplant, as regards preaxial and postaxial borders, depended upon the original orientation of the graft. In this case, selected as a type of the usual experimental finding, the Anlage possesses the power of "self-differentiation," to use the language of Roux—that is to say, it grows and continues to unfold by its own inherent impulse. In the development of the prostate gland, on the other hand, we have a case of "dependent differentiation," in which the power of unfolding to completion does not wholly reside within the Anlage. In the differentiation of the prostate a moulding influence, specifically hormonic and external to the organ itself, comes into play.

In respect of the secondary sexual characters, castration, whether of a male or of a female vertebrate, produces a common "neutral" or "indifferent" type of animal, and Steinach has shown that by experimental interchange of gonads it is possible to "masculinize" an originally female and to "feminize" an originally male animal. Thus castration and implantation of an ovary into a male guinea-pig lead to marked growth and differentiation of the mammary glands, while implantation of a testis into a spayed female leads to a penile enlargement of the clitoris. Lipschütz (1919) in a special investigation of the last-mentioned change finds that corpora cavernosa make their appearance in the clitoris of the inverted guinea-pig and also special horny spikes characteristic of the guinea-pig penis. In the formation of these corpora cavernosa and horny spikes we have an experimental case of moulding by the environment, for in the absence of the hormone from the male interstitial gland they do not develop, the clitoris remaining a clitoris. As establishing actual homoplasy with the corresponding structures of the male penis, Lipschütz (1924) has also shown that the development of the horny spikes in the penis of a male guinea-pig depends upon the testicular hormone.

Other cases of homoplasy have also been induced experimentally. In the development of the vertebrate eye it has long been known that the essential parts arise from two separate Anlagen; the light-recipient apparatus or retina as a hollow protrusion of the brain, which, becoming invaginated, forms the optic vesicle; the main light-refracting apparatus or lens as an ingrowth of the skin. The development of the optic vesicle proceeds by self-differentiation; when it is dissociated from any connection with the brain it forms a complete retina (W. H. Lewis, Spemann). The development of the lens is a case of dependent differentiation; in the absence of the optic vesicle it fails to

differentiate. If in a larval amphibian the skin overlying the optic vesicle is removed and replaced by skin from any other part of the body, a perfect lens is formed by the transplanted skin (W. H. Lewis). Furthermore an optic vesicle, grafted into an abnormal site, proceeds to modify the overlying skin so that it becomes a lens. In this case the influence exerted at close range by the optic vesicle upon the indifferent skin tissue is not simply that of a chemical messenger or hormone; something more suggestive of physical moulding must come into play, otherwise it is hard to conceive how the proper amount of (indifferent) tissue is selected and adjusted to fit the mouth of the vesicle.

While we have merely touched on the fringe of this more modern line of investigation, the instances given suffice to show that the moulding influence of the internal environment of an Anlage that is not self-differentiating has been brought within the scope of experimental study. In our selected cases the decisive influence exerted upon the non-self-differentiating Anlage has been proved to have its seat in one single primary or controlling organ (or Anlage), to which the other is secondary or subservient—in which respect Lankester's supposition of plasis is rendered less vague, more definite. Even in cases of this order of simplicity, where, during ontogeny, we see a direct and all-powerful reaction of one single organ upon another, the physical means of interaction between the pair of correlated organs is not the same in every case. This must be kept in mind when we come to deal with the exceedingly difficult cases of phylogenetic moulding or adaptation.

SPEMANN'S CRITICISMS OF THE HOMOLOGY CONCEPTION

In a special article on the vexed subject of homology Spemann (1915) has utilized some of these experimental results to criticise not only the conception of homology in itself but also, apparently, Lankester's distinction between homogeny and homoplasy.

Citing his own experiments and those of Lewis on development of the lens, he points out that the lenses in the experimental cases are not homologous with normal lenses; nor are they homogenetic; they are, however, homoplastic. But, he says, the experiments also lead inevitably to the conclusion that lenses formed in normal development are both homogenetic and homoplastic, whereupon he feels constrained to ask whether Lankester's distinction has any deeper meaning.

This obscure remark seems to mean one or other of two things. Either Spemann has failed to understand Lankester, or, reflecting on the bearing of his own experiments, he has been momentarily waylaid into a pessimistic, *cui bono?* frame of mind. We can hardly believe the latter, i.e., we can scarcely suppose that he doubts the fact of homogeny (he does not doubt homoplasy). The valid examples of homogeny are the group features common to two or more great assemblages of animals by which is determined their subordination under a common category. It is the steady and extraordinary persistence of structural similarity under all apparent disguises, under all variety of environment and adaptation, that created the science of morphology to begin with, and that later provided the chief argument for common descent and furnished the means for a natural classification of animals. Homogeny with its very specific implications is not a thing of moonshine. We are left to suppose that Spemann has simply misread his authority. Now, Lankester has well foreseen that homoplasy may in some cases coincide with homogeny, as

the following sentence shows: "Further, if, instead of similar parts in the same organism, we suppose the same forces to act on parts in two organisms, which parts are exactly or nearly alike and sometimes homogenetic, the resulting correspondences called forth in the several parts in the two organisms will be nearly or exactly alike." Not the least striking feature of Lankester's homoplasy is that, enunciated in 1870, it should now have been so aptly confirmed by experimental work.

Going farther than Haeckel, who gave expression to a similar difficulty, Spemann says, "In point of fact, when one probes more closely, it is perhaps in the rarest cases possible to decide with certainty whether homology or analogy is involved." Here of course he refers, not to the structural similarities between functionally equivalent organs of widely different forms (the classical cases of analogy), but to the multitude of finer structural correspondences between the parts of more closely related forms. While his statement is a qualified one, it is of interest as representing the new outlook that comes of experimental handling of the problems of bodily structure. A mere assertion of homogeny no longer suffices to account for a structural correspondence. Homoplasy, all unsuspected, may have been simultaneously at work.

When Spemann finally concludes that "the homology conception as understood during the historic period goes to pieces in our hands when we try to work with it in the causal sphere," he means simply to say that, notwithstanding all its past achievements, as an engine of further investigation it requires now to be supplemented by something more definite and determinate, something we can grip without the feeling that the instrument we hold is an insecure or wobbly one. No one will doubt that for preliminary, provisional determination of the major relationships of animals one to another, the conception of homology has been of incalculable service. It is when we come to examine into the *mechanism* underlying similarity or divergence, as the case may be, that the need of some further means of assistance becomes felt.

HOMOLOGY AND FUNCTION B

As we began the subdivision of this article by discussing physiological considerations, so it is proper that we should return to physiology before its conclusion. It will have become apparent that homology and similarity as regards Function *B* as a rule coincide. The question now arises: Do they always coincide? As test cases let us consider some examples.

The thyroid. Throughout the Vertebrata proper (Pisces, Amphibia, Reptilia, Aves, Mammalia) this ductless gland has the same essential structure, consisting of closed vesicles, in which a single layer of epithelium as a rule surrounds colloid material. Throughout the group it preserves the same topographical position and has the same embryological history, viz. it arises as a median ventral downgrowth from the pharyngeal entoderm between the first and second branchial pouches, i.e., about the level of the first aortic arch. Its functional attributes are equally uniform and distinctive. It shows a great avidity for iodine introduced into the circulation; it elaborates a highly specific substance, thyroxin, which contains iodine in organic combination and whose chemical constitution has not been completely elucidated. In its peculiar avidity for iodine and in the manufacture of thyroxin, its Function *B* may (in a measure) be said to be determined, for, apart from scattered portions of similar and similarly derived tissue in the region

of the neck, we know of no other gland that exhibits the same biochemical characteristics. Within the limits of distribution aforesaid we may therefore say that the thyroid gland displays a striking accordance of homology and Function *B*.

Comparative anatomy has however pushed the "homology" of the thyroid beyond the limits of the Pisces into the lower Craniata, or cyclostomes, into the Acrania (*Amphioxus*) and into the Urochorda or tunicates. Adult cyclostomes have a true thyroid; in the larval cyclostome, *Ammocoetes*, the thyroid is represented by a complicated glandular structure of unknown function, the endostyle organ, which opens into the pharynx by a wide duct, and from which at metamorphosis the thyroid follicles of the adult are derived. In close details of structure as well as in its topography the endostyle organ of *Ammocoetes* corresponds with organs of similar name in *Amphioxus* and in tunicates (cf. D. Marine). The greater elaboration of structure of the endostyle organ, coupled with its free communication to the pharynx, undoubtedly indicates a difference in its intrinsic mechanism as compared with that of the thyroid.

Dismissing from our minds the unusual interest and suggestiveness of this particular morphological finding, let us confine ourselves to the purely formal question with which we started. It is plain that while the endostyle organ of these three types may be said to be homologous one with another (and then chiefly in the sense of positional homology), one cannot assert that the endostyle organ itself is, in any received sense of the word, homologous with the thyroid. We should rather phrase the matter by saying that the thyroid of the adult lamprey finds its Anlage in some part of the endostyle organ of *Ammocoetes*, or simply that the thyroid is a derivative of the endostyle organ. Just at the point, therefore, where the word homology proves inappropriate to express the nature of the relation, a difference in respect of Function *B* makes its appearance.

The medullary tissue of the adrenals. The adrenal glands of mammals, consisting of two parts, cortex and medulla, have a complex mode of development. The cortex, homologous with the interrenal body of elasmobranchs, arises from mesoderm cells of the genital ridge. The medulla, represented in fishes by the segmentally arranged "paired bodies," is derived from cells which belong to the same neuroblast masses as give rise to the nerve cells of the sympathetic ganglia. Throughout the group of the Vertebrata this medullary tissue presents the appearance of an endocrine organ. It strikes a brownish yellow color on treatment with salts of chromic acid (chromaffin reaction) and on extraction yields a hormone, adrenaline, whose chemical constitution has been fully determined. The hormone, from whatsoever vertebrate derived, exercises in mammals very specific pharmacological effects, which are the same as those produced by electrical stimulation of the nerves of the thoracico-lumbar sympathetic outflow. Here, therefore, we have a case of morphological or embryological homology with (so far as tests have hitherto gone) complete similarity of intrinsic physiological mechanism throughout the vertebrate group.

Islet tissue of pancreas. Among the secreting alveoli of the pancreas of vertebrates, and derived from the same endodermal Anlage as the pancreas, are multitudinous patches of a peculiar variety of tissue, the so-called islets of Langerhans. The cells of this tissue, which show affinities for particular stains and are of two recognisable types, have no

acinar formation, their disposition and vascular arrangements suggesting an endocrine function. In teleost fishes the islet tissue is particularly distinct, being encapsuled and occasionally present in masses of considerable size, which permit of ready isolation from the rest of the pancreas; in other vertebrates the islet tissue is intermingled with the alveolar. In its topographical arrangement, in its structural characters, and in its embryology, this islet tissue is similar or homologous throughout the group.

The functional attributes of this tissue are also distinctive and specific. No matter from what vertebrate it is obtained, an extract of the material lowers the percentage of sugar in the blood, promotes storage of glycogen in the liver of a diabetic and allows of utilization of glucose by the tissues, in virtue of which actions it can temporarily restore to normal the defective carbohydrate metabolism in cases of diabetes mellitus. At one time it was claimed that the islet tissue is merely a functional phase of the alveolar epithelium of the pancreas, that it can be transformed into alveolar epithelium and vice versa; all the available evidence goes however to show that while the two varieties of tissue owe their ultimate origin to one and the same mesoblastic Anlage, an early differentiation occurs, the one form becoming quite distinct from the other, with no possibility of reciprocal transformation (see Bensley). The two varieties of tissue are structurally and developmentally distinct and independent, and their functional attributes are similarly distinct and independent.

The foregoing examples of endocrine organs have been cited, partly because of the precision with which we can characterise their respective activities, partly because of the abundance, unusual in a physiological question, of comparative experimental data. Other endocrine examples, less definite in detail but all pointing in the same direction, might have been adduced. It will be noted that the criterion of similarity in respect of Function *B* on which we have relied is identity of a highly specific chemical or pharmacological product. The criterion itself is not beyond cavil; from industrial chemistry one might furnish endless illustrations of identity of product based on entirely different manufacturing processes, i.e., on entirely different intrinsic mechanisms; furthermore, we know that closely similar biochemical products, e.g. diastatic and proteolytic ferments, may be elaborated by very different types of organism, vegetable and animal, and therefore quite conceivably by different intrinsic mechanisms. In a difficult and involved scientific question it is sometimes possible however to err in the direction of undue caution. Most people would probably be willing to concede that in the cases cited the test of identity as regards Function *B* is appropriate and adequate.

The poison-glands of snakes might also be cited as organs whose mechanism is in a way particularised by the peculiar pharmacological products they yield. The active constituents of a venom are bodies allied to proteins, any given venom being a complex mixture of different albuminous toxins, which, roughly separable by physical or chemical means, are distinguished one from another as yet only by biological test. Two main categories of snake-poison, colubrine and viperine, are recognized by their action, but the pharmacological distinction between them is not hard and fast like the naturalists' distinction between the group of viperine and the group of poisonous colubrine snakes from which they are in each case derived. Apart from other poisons of animal origin, it may be said

that no pharmacological substances exhibit exactly the same array of biological reactions as snake-venoms; in other words, they are specific or distinctive products. It has often been stated that the poison-glands of snakes are homologous with the parotid glands of mammals, and this particular example was long considered by the author as a crucial case, rendering untenable the supposition that homology and intrinsic functional mechanism always coincide. Owing to their different innervation the venom-glands of snakes are now known not to correspond to the parotid gland of mammals. As to their origin, Wiedersheim says that they "become differentiated from" the upper of the two pairs of labial mouth glands common to reptiles. We thus see that in accordance with the individuality of their intrinsic functional mechanism they have no known homologues in other animals.

The cerebral cortex. As another case let us take the grey matter on the surface of the mammalian cerebrum, the so-called cerebral cortex. This is spread over the surface in a layer whose thickness and general cellular composition present an appearance of unusual uniformity. At the same time experiment has displayed a definite association of particular functions with particular areas of the cortex, one region controlling voluntary movements of different parts of the body, another being concerned with conscious vision, another with hearing, and so on. It is plain that the intrinsic mechanism of these different regions must vary. An area whose duty is to control voluntary movement must differ in ultimate action from one which receives and interprets visual impressions. One of the achievements of recent histological examination, beginning with Cajal and continued by A. W. Campbell and by Brodmann, has been to show that on a basis of simple histological structure the cortex may be mapped into a large number of regions, each with its own distinctive characters. Instead of being of uniform texture it is a mosaic of areas of different histological pattern. While this field of tedious and time-consuming histological work is as yet in its infancy and hard and fast statements can scarcely be made, in two cases at least, viz. that of the motor region and of the visual region, the limits as histologically defined correspond with those experimentally determined.

The facts with regard to the motor area are of especial interest in this connection. At quite an early period of investigation of cerebral localization Bevan Lewis and Henry Clarke, on the basis of a histological difference between the pre-Rolandic and the post-Rolandic cortex, concluded that the motor region proper lies in front of the fissure of Rolando. This deduction did not agree with the findings of subsequent experimenters, who, using strong electrical stimulation obtained motor effects on excitation of the cortex both behind and in front of the Rolandic fissure. The histological communication of these authors was in consequence ignored. Grünbaum and Sherrington, employing a more refined experimental technique, eventually proved that the motor area is strictly limited to the pre-Rolandic region. In this case histological differentiation between two areas had been able to indicate differences in their function which took more than twenty years fully to confirm. J. S. Bolton by histological methods first determined the exact limits of the visuo-sensory area of the cortex, which limits corresponded with those already established by the method of combined stimulation and ablation.

We should have no hesitation in naming

the motor, the visual or the auditory region respectively of the brain of man and of anthropoid apes as homologous each to each. They have homology of position, homology of development, and, as the investigations of A. W. Campbell show, they have in each case essential identity of intimate structure. As we cannot doubt that their intrinsic cellular mechanism is in each case of similar character, this example also goes to show that homology and Function *B* invariably coincide.

An additional criterion of homology. The truth is, wherever we inquire, the vaguely defined thing that we call homology implies identity of intrinsic mechanism in the homologous parts. We thus obtain a new—and, be it noted, a very sharp—criterion of homology, based not on position nor on embryological evidence, but on physiological similarity, and the test of such similarity is an experimental one. When Geoffroy in his notable attempt to clarify the problem of morphology discarded analogy, he was guided by a true instinct. Not so, when in his ignorance of the potentialities of physiology he waved all physiological considerations aside. His connection with the problem is merely a fine example of the thesis, elaborated by Sir J. G. Fraser in his "Psyche," that methods and institutions in themselves open to patent objection may at an early phase of culture exercise a very wholesome and salutary effect.

The new criterion applied to classification. It were tempting at this juncture to stop and point out that in the classification of animals considerations pertaining to Function *B* can furnish significant and suggestive data. Without even specifying any of the usually cited facts of formal structure one might define the group of Vertebrata, for example, in terms of common erythrocytic, common splenic, common thyroid, common pancreatic-insular, common adrenal, common hypophyseal and common labyrinthine function; the Tetrapoda in terms of superadded parathyroid and, possibly, bone marrow function; the combined group of Sauropsida and Mammalia in terms of the common maintenance and attachment function of their stratum corneum; the Sauropsida in terms of common purin metabolism; the combined group of Aves and Mammalia in terms of common homoiothermism; the Mammalia in terms of common lacteal function; the Eutheria in terms of common luteal function. Similarly with other animal phyla and their subdivisions. The systematic textbooks of the future will no doubt develop and extend these physiological criteria of resemblance and of difference. When, too, it has once become possible to interpret the physiological significance of the various combinations of structural characters that now define the different animal groups, our present systems of classification will take on a new meaning. For the present, however, it is more important to proceed a stage further in our inquiry with regard to the specific problem at issue.

ONTOGENETIC AND PHYLOGENETIC FLUX

It has been pointed out how the new science of embryology introduced into the problems of morphology the idea of flux. No sooner had embryology become well established than Darwin imported into the subject still another fluxional conception. The various animal species, having evolved from ancestral forms dissimilar to them, are not themselves fixed or static entities. Rather, they represent temporary phases in a continuous line of progressive change. Morphology has thus to take cognisance of ontogenetic flux and of phylogenetic flux.

The homology conception arose when animal forms were believed to be fixed or static. The introduction of embryology failed in any way to modify the conception of homology. The embryological criterion of homology was not due to embryology as such.

With the advent of Darwinism a forward step was made. In its implications for morphology ontogenetic flux was now for the first time taken into practical account. An attempt, confused but still definite, was made to incorporate "embryological homology" as a method into the working equipment of the subject. The recognition of phylogenetic flux led at first to no new practical method of its own, just as the introduction of embryology on a previous occasion led to no new morphological method.

Lankester's effort was both critical and constructive. His homogeny is static, much as the primitive positional homology was static. The recognition of plasis, limited as was the use he made of the idea, is his important contribution to the conception of organic flux, and in the very general terms of its formulation his homoplasy is applicable both to ontogenetic and to phylogenetic flux. Later came *Entwicklungsmechanik* with its strictly ontological experiments, which on ontological territory have confirmed and rendered much more definite Lankester's hypothesis.

With it all, we still lack a means of treating phylogenetic flux, which, be it noted, is the great outstanding problem of formal morphology. In this type of flux we recognize the occurrence of two quite different things. One is modification of existing structures by way of adaptation to new uses; throughout these modifications the intrinsic mechanism remains essentially the same and the parts remain homologous. The other is the invention or evolution of structures of a quite new type, whose intrinsic mechanism is also new. It is true, the new structures, which show novel biophysical or biochemical behavior, themselves grow out of the old. While the process by which they are produced is entirely obscure, their apparition denotes a different kind of event from any simple successful application of an existing structure or system of existing structures to a new purpose.

Distinct as the foregoing two problems are—that, namely, of modification by simple adaptation and that of brand new invention—both are problems of plasis in a wide sense. It should always be kept in mind that homoplasis or analogy is only one limited aspect of a more comprehensive plasis. Analogy, notwithstanding its great and unexploited potentialities for the study of plasis, is, so to speak, an accidental affair. Only in certain cases will the modifications achieved in two different forms closely resemble each other.

Exclusive preoccupation with the homology method has been responsible for a certain narrowness of vision among those who handle animal structure. There has been a tendency to consider animals merely as ringing the changes on a fixed or preordained equipment of structure. Bateson was the first to push this philosophy to its logical conclusion and to assert, with what degree of conviction no one can quite make out, that evolution proceeds by dropping of characters rather than by acquisition of new characters. Of course, this whole philosophy is wrong. The inventiveness of animals is not exhausted in the extraordinary way in which they can bend or mould existing equipment to new uses. They can equally well, departing from precedent, hammer out inventions of a

kind that is entirely new, and this they have done over and over again.

While no one would dispute that the science of morphology has been erected on the conception of homology, it is also clear that the help obtainable from homology in any study of animal structure is of a restricted kind. Homology is at best an inference originally forced upon comparative anatomy by its material. It is an inference that arises mainly from similarities; from dissimilarities only in so far as these serve as a background or contrast to the similarities. Practically speaking, it is an effective method of classification. It serves to disentangle any large assemblage of forms and to group structurally similar forms under common categories. Rationally speaking, it does not in any way explain the similarities which gave it birth. Even for purposes of classification it has been of assistance only in laying down the broad features of similarity of the larger groups. It has been of little real service in assessing the nature of the gaps between widely divergent types. For finer familial, generic and specific distinctions it is scarcely ever used, because it does not profess to deal with dissimilarities. At the same time our whole knowledge of evolution, which is fundamental for any science of animal structure, teaches us that a critical phase of the evolutionary process lies in the origin of varieties and of new species.

Because homology, and for that part analogy, deal only with similarities, they are both defective principles in the face of developing diversity. As divergences arise not discontinuously but by slow gradation (we are now speaking in phylogenetic terms and are not raising the issue of mutations, which from our present point of view is a secondary matter), it is clear that simple static homology and analogy do not provide any infinitesimal calculus that can be applied to the question of flux, i.e. to the birth and continuous development of dissimilarity. If the systematic study of structure is to go on advancing, homology must be reinforced, analogy, in its limited field of operation but from the plastic point of view, must receive its full meed of consideration, while attention must be directed to differences as much as to similarities.

Experimental embryology has already applied itself to the problem of ontogenetic flux. Except by implication it has not touched upon phylogenetic flux. We are aware that phylogenetic flux in some way dominates and sets the character of ontogenetic flux. So far as one can say, it is primary, ontogenetic flux being secondary. For the intimate study of phylogenetic flux the one ready instrument to our hand is physiology. An example or two may suffice to illustrate the matter.

The sulcus lunatus of the Chinese brain. By gross examination of the sulci and of the sectioned cortex, Shellshear has recently shown that the occipital region of the Chinese differs as a rule from that of the European brain. In the Chinese brain a clearly marked sulcus lunatus or "Affenspalte" extends well out on to the lateral surface of the occipital lobe. In most cases its posterior lip forms an operculum, and the stria of Gennari, which characterises the "visuo-sensory" region of Bolton, extends to the posterior lip of the sulcus. Thus in the Chinese brain the stria of Gennari, instead of being limited to the mesial aspect of the occipital lobe as in Europeans, spreads on to the lateral aspect. It is a common saying among the Chinese themselves that their vision differs from that of Europeans. In looking directly forward they claim to have a clearer perception of what is

happening in the peripheral field of vision than do Europeans. Their art objects too are more crowded with detail than are the corresponding productions of the white races of mankind. It is true that Shellshear in his purely anatomical exposition refrains for the moment from making any functional comparison, but if some difference of the kind indicated should also be found by appropriate physiological experiment to exist between Chinese and Europeans, it is plain that we should here have a means of observing and tracing structural and functional flux within the limits of one and the same species. The numberless recorded observations of anatomical differences between the different races of mankind have also no doubt their functional counterpart, though methods of experimental comparative treatment are as a rule less immediately obvious than in the particular case just cited.

The odor-secreting glands of mammals. In his article, "Mammalia," in the ninth edition of the *Encyclopaedia Britannica* Flower has collected together a list of odor-secreting glands connected with the skin of various mammals. His statement is as follows: "To this group of structures belong the suborbital gland or 'crumen' of Antelopes and Deer, the frontal gland of the Muntjak and of Bats of the genus *Hipposiderus*, the submental gland of the Chevrotains and of *Taphozous* and some other Bats, the post-auditory follicle of the Chamois, the temporal gland of the Elephant, the lateral glands of the Musk-Shrew, the dorsal gland of the Peccary, the inguinal glands of Antelopes, the preputial glands of the Musk-Deer and Beaver (already alluded to in connection with the use made of their powerfully odorous secretion in medicine and perfumery) and also of the Swine and Hare, the anal glands of Carnivora, the perineal gland of the Civet (also of commercial value), the caudal glands of the Fox and Goat, the gland on the humeral membrane of Bats of the genus *Saccopteryx*, the post-digital gland of the Rhinoceros, the interdigital glands of the Sheep and many Ruminants, and numerous others. In some of these cases the glands are peculiar to, or more largely developed in, the male; in others they are found equally developed in both sexes." In this striking series any question of homology between the different glands is excluded because of topographical reasons. Yet the glands in question form a related group, being derivatives presumably of sebaceous glands and subserving somewhat similar uses. At the same time each is obviously an independent invention, and the odors or chemical products elaborated differ one from another. How should one set to work to extract from such a series further information respecting phylogenetic flux? Clearly one must first invoke physiology and biochemistry.

The great trouble with morphology as a guide in the elucidation of animal form, or even as a means of approach to structural and evolutionary problems, is that it is silent as to the mode of operation of the structures with which it professes to deal. Imagine a refined morphology of the brain of mammals, based purely on comparative criteria gross and microscopic, but which fails to envisage the experimental results of the workers on cerebral localisation, ranging from Fritsch and Hitzig to Henry Head, or of the workers on cerebral "educability," from Goltz to Pavlov! The one thing that gives life and meaning to the comparative anatomical knowledge of the cerebrum and saves it from being an arid collection of maps and diagrams, is the physiological work that has proceeded *pari passu* with the anatomical. Indeed the time and ef-

fort spent on the details of neurological anatomy is justified only when the work is meant to be brought into correlation with the physiological. What holds true of a pure morphology of the brain holds equally true of morphology generally. Morphology finds a meaning only in its functional setting. At our present stage of history it is easy for us to see that the original decision to separate physiology from comparative anatomy was foredoomed to failure.

PLASIS

In view of the preceding exposition it is plain that the broad process here called plasis, the process to whose investigation the experimental embryologists have already devoted themselves in the field of ontogeny, is equally insistent in the realm of phylogeny. We have seen how Lankester, a Darwinian and believer in natural selection, was early constrained to postulate special environmental "forces" in order to account for certain aspects of phylogenetic plasis. There can be little doubt that plasis is a controlled process and proceeds according to law. Granted the fact of evolution, the astounding fit between the animal as a whole and its environment, and the correspondingly wonderful internal adjustment of all its diverse parts one with another, seem to indicate the operation of (physical) law. Endlessly complex as animal structure is, the dominant principles involved in maintaining the structure or in changing it according to need, may be few and relatively simple.

Roughly speaking and without attempting at the moment any further sifting of detail, we may recognize three (or four) elements in phylogenetic plasis: (1) the power to transmit by heredity the temporarily existing condition of structure; (2) adaptive modification of existing structure; (3) the invention of new structures; to which we may add, whether an independent thing or not, (4) the occasional dropping of existing characters. Thanks to the work of the school of T. H. Morgan and to the investigations of Goldschmidt, our knowledge of the mechanism of (1) is rapidly becoming more precise and definite. We may also have some possible knowledge of the mechanism of (4), but scarcely yet of (4) in its adaptive implications. The conditions that control (2) and (3) remain quite obscure, and these are the very elements that have not yet been subjected to the rigorous physiological mode of inquiry. Lucas has sought to sketch a method whereby one might begin with the investigation of (3). In the course of our present exposition we have obtained a physiological test for homology, which implies that we have a better means than before of observing the operation of (2).

The failure up to the present to establish by experiment the transmission of "acquired" characters may well be due to the paucity of our knowledge respecting (2) and (3). It has often been suggested that our laboratory attempts to cause phylogenetic modification may not have taken account of an adequate time factor. Apart from the question of time there is another possible way of looking at the matter. Any given animal is a system in equilibrium with its environment, and is built up of a vast congeries of systems all in equilibrium with each other. To use a very rough illustration, the organism might conceivably be likened to a complex jointed linkage, which is poised or balanced at some central region, all its various outlying parts being similarly poised but so interconnected that an adequate disturbance of one or more may cause a rearrangement of the whole with

consequent new position of total equilibrium. In each kind of animal this complex equilibrium is different; in any two closely related species the equilibrium has taken a different cast or set; and the differences increase as we pass in succession from the species to the genus, from the genus to the family, and so on. We know, too, that these equilibrium differences are even tied up with chemical differences in the body proteins of the various organisms. Now, experience has amply taught us that the structural parts of any animal may be crudely mutilated without damage to the essential, specific or phylogenetic, equilibrium. So, too, did the atoms of terrestrial chemistry remain in equilibrium, notwithstanding all kinds of apparent rough usage, until Rutherford discovered a means of bombarding them in a special way. We may not yet have hit upon the proper type of bombardment effectively to upset the specific or phylogenetic equilibrium. We may not be clear as to what constitutes an acquired character in the sense of phylogenetic modification, and in our experimental attempts at phylogenetic modification we may have been dealing only with trivial characters, not with any of the pivotal equilibrium-deciding factors.

Mere speculation is however a profitless matter. Enough has perhaps been said to enable a physiological reader to realize that his subject is intimately involved and can render important assistance in some of the wider issues concerning comparative anatomy and the process of evolution. The great service rendered by comparative anatomy, apart from furnishing material in proof of evolution, has been to raise problems which it does not of itself possess the means of solving. Without recourse to experiment the ultimate issues must necessarily remain unsettled. The eventual solution of the broad problem of adaptation, or what we have here called plasis, would seem to lie with the physiologist, provided only that he were willing to give his deliberate attention to comparative problems. It might equally be with the comparative anatomist, provided he should adopt the discipline and the methods of physiology.

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THE HISTORY OF WHALES—THEIR ADAPTATION TO LIFE IN THE WATER (*Concluded*)

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PLATANISTIDAE

THERE does not appear to be any single directive trend in the line of development that regulated the overlapping or telescoping of the major bones in the odontocete skull, but on the contrary telescoping has given rise to many different types of skulls, and of these none are more unusual than that of the Maryland Miocene porpoise, *Zarhachis flagellator* (Kellogg, 1924; 1926). An extreme stage in the lengthening of the rostrum is represented by this skull, and appears to mark the culmination of the long-snouted type of porpoise. The skull is nearly four feet long with the rostrum fully five times as long as the braincase. Mechanical difficulties would interfere with a further lengthening of this type of rostrum. While the family position of this porpoise may be a matter of personal opinion, the periotic bone is similar to that of *Platanista*, and cranial peculiarities also indicate that it should be referred to the family Platanistidae.

According to our present knowledge, *Zarhachis flagellator* represents a highly specialized aberrant type that possesses certain fundamental characters in common with the living Ganges porpoise *Platanista gangetica*. No fossil porpoises of this type have been described from Miocene formations of Europe and it may have been a migrant from some other region, possibly the South Atlantic, which came into association with the more widely distributed types during the latter part of the Miocene period. In its general features the skull of *Zarhachis* is characterized by the presence of a pair of crescentic orifices inclosed by ectethmoids on the anterior wall of the braincase; maxillaries expanded laterally behind the antorbital notches with their lateral borders turned upward to sheath the internal surfaces of the up-built supraorbital processes of the frontals, and in contact posteriorly with the supraoccipital; small elevated vertex; pterygoid with well developed external reduplication, which extends from the squamosal to the median line of palate at a level considerably in advance of antorbital notch, concealing the alisphenoid and palatine bones; palatine bone forming part of the anterior wall of narial passage; total number of teeth in excess of 300; the enamel crowns of teeth ornamented with longitudinal striae and the roots slightly thickened. The symphysis is equivalent to more than two-thirds of the total length of either mandibular ramus. The cervical vertebrae are free, and the dorsal and lumbar vertebrae have broad flattened neural spines. The path or paths of development followed by the descendants of this extinct porpoise are unknown at the present writing.

The existing *Platanista gangetica*

undoubtedly traces its origin back to some extinct porpoise in which the outer borders of the maxillaries were turned upward above the orbits. This peculiar structural condition permitted the maxillaries to grow upward, resulting in the formation of the odd incurved fan-like maxillary structures seen in the living *Susu*, which cover the facial depression like a mask. The rostrum is so slender and the palate so narrowed that the upper tooth rows lie side by side, and in old individuals apparently merge together at the posterior end of the series. The anterior teeth have a high pointed crown and a broad laterally compressed root. The relations of the basicranial bones suggest that the rostrum and braincase have been telescoped to a greater extent and in a somewhat different manner than in other porpoises. To recapitulate the evidence supporting this observation it may be pointed out that in correlation with the depression of the rostrum below the level of the braincase, the narial passages have moved backward and are situated on a level with the anterior margins of the squamosals, the pterygoids

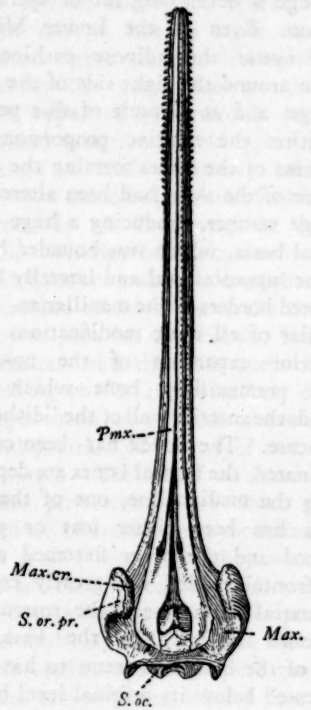


FIG. 12

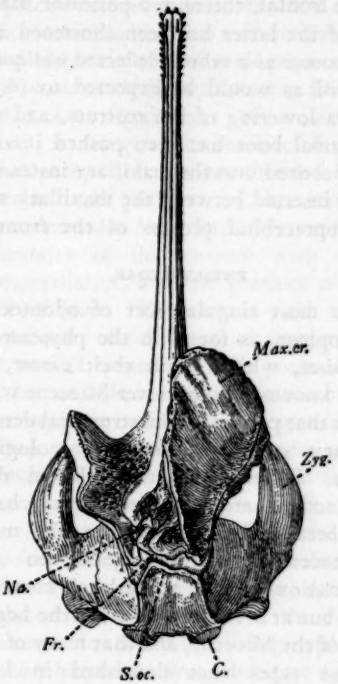


FIG. 13

FIG. 12. DORSAL VIEW OF SKULL
Zarhachis flagellator, Middle Miocene, Maryland

FIG. 13. DORSAL VIEW OF SKULL
Platanista gangetica, India. Left maxillary crest removed to expose upper surface of cranium

and their external reduplications extend forward to the level of the antorbital notches and thus entirely conceal the palatine and alisphenoid bones, the opening for the infraorbital canal is within the temporal fossa, the zygomatic process is placed far forward and its extremity is in contact with the supraorbital process of the frontal, the antero-posterior diameter of the latter has been shortened and the process as a whole deflected obliquely forward as would be expected to result from a lowering of the rostrum, and the lachrymal bone has been pushed inward and mortised into the maxillary instead of being inserted between the maxillary and the supraorbital process of the frontal.

PHYSETERIDAE

The most singular sort of odontocete development is found in the physeteroid porpoises, which begin their career, so far as known, in the Lower Miocene with skulls that possess all the structural details of their successors in later geological stages. It is confidently believed that these somewhat generalized sperm whales had been differentiated from the main odontocete stock subsequent to the elimination of the postorbital constriction, but at a time long before the beginning of the Miocene, and that many of the diverse types that flourished in later Miocene seas trace their ancestry back to as yet unknown types of extinct physeteroids. The living sperm whale (*Physeter catodon*) has an enormous reservoir on the top of the head, surrounded by a fibrous integument, and divided interiorly into compartments, which communicate with one another and with cells or sinuses also filled with liquid oil or spermaceti. Beneath this reservoir, which may contain 10 to 15 barrels of liquid oil, is a great mass of fibrous cellular tissue, likewise saturated with spermaceti, known as the adipose cushion. Spermaceti, however, is not always present, for occasionally cachalots are killed that are "dry." If any reliance may be placed on analogous structural conditions in the living sperm whale the structural details of these early physeteroid skulls had been adjusted to lodge a developing fat or spermaceti cushion. Even in the Lower Miocene *Diaphorocetus* the adipose cushion had grown around the right side of the narial passage, and as a result of this peculiar condition the relative proportions and relations of the bones forming the dorsal surface of the skull had been altered in a strange manner, producing a huge supracranial basin, which was bounded behind by the supraoccipital and laterally by the elevated borders of the maxillaries. Most peculiar of all these modifications is the posterior expansion of the up-curved right premaxillary bone which overspreads the anterior wall of the "dished-in" braincase. The vertex has been entirely eliminated, the frontal bones are depressed along the median line, one of the nasal bones has been either lost or greatly reduced and the other flattened against the frontal behind the greatly enlarged left narial passage, and the rostrum has expanded laterally at the base. The roof of the braincase seems to have been depressed below its original level because of the additional weight and pressure of the developing adipose cushion.

The oldest known Miocene physeteroids as well as some of the later ones have teeth implanted in distinct alveoli in the maxillary and premaxillary bones. The premaxillaries form the extremity of the rostrum, and three teeth are implanted in each bone. In the course of geological time we observe that there is a tendency among certain types for the teeth to become loosely implanted in rather large alveoli, and this condition is accompanied

by a corresponding decrease in the thickness of the intervening septa. These septa finally disappear, leaving an open alveolar gutter in the maxillary. The growth of the maxillary teeth is arrested, and a hypertrophy of the dentition ensues. Functional teeth are not present in the upper jaw of the living sperm whale, *Physeter catodon*, but as many as eight atrophied teeth are sometimes found buried in the gum. Conversely other extinct types of physeteroids retain a functional dentition in the upper jaws to the close of their relatively brief life span. The mandibular teeth of all known physeteroids are implanted in distinct alveoli. Whether or not a narrowing of the mandibular symphysis brought about an increased effectiveness of the teeth in the lower jaws no one knows, but it is nevertheless true that the great lateral broadening out of the maxillary carried the upper tooth rows outside of the normal occlusal position of the upper and lower cheek teeth. The teeth of these early Miocene physeteroids are much larger than those of contemporary odontocetes, and it would seem that they were employed as much for tearing as for seizing. Killer whales (*Orcinus*) tear away portions of the flesh of their victims by quick powerful jerks, and it is quite probable that the earlier sperm whales tore their food apart in a similar manner. It is evident that the earlier Miocene delphinoids were likewise predacious, but their slender teeth were adapted for seizing and holding slippery prey, such as fish.

Two skulls, representing different genera of physeteroids, are known from the Lower Miocene Patagonian formation exposed along the coast in Chubut Territory, Argentine Republic. The smaller of these, *Diaphorocetus poucheti* (Moreno, 1892) measured when complete about three feet in length. It possessed teeth in both jaws, for which there were more than 14 alveoli in each maxillary bone. The occiput of this skull is obliquely truncated, each maxillary bone is perforated by large foramina along the lateral crest, the postnarial portion of the right premaxillary is broad, forming the medial surface of the posterior wall of the supracranial basin, and the lateral margin of the maxillary is not excessively thickened above the supraorbital process.

The other skull, representing *Idiorophus patagonicus* (Lydekker, 1894; Kellogg, 1925), is nearly twice the size of that of *Diaphorocetus*. It is characterized by the number and position of the maxillary foramina, the long laterally compressed extremity of the rostrum with arched premaxillaries, and the presence of teeth in both jaws. There are 22 teeth in each upper jaw, of which 19 are implanted in the maxillary and 3 in the premaxillary. Each mandible is provided with 24 teeth. The teeth average a little more than 4 inches in length, and their conical crowns are covered with rugose enamel. The long, terete, and but little curved crowns are equivalent to a little more than one-fourth of the total length of the teeth.

The reduction of the maxillary dentition had commenced as early as the Middle Miocene, for we have indisputable evidence that such was the case in the Temblor *Aulophyseter morricei* (Kellogg, 1927) found near Bakersfield, California. The shallow closely approximated alveolar grooves of the Temblor skull, occurring as they do with other cranial details that undoubtedly indicate a more advanced stage in the basining of the facial region, have suggested the possibility that if teeth were present in the upper jaws they were lodged in the gum as in the living sperm whale. The skull measures about four feet in length, and the distal constriction of the rostrum is coextensive with the

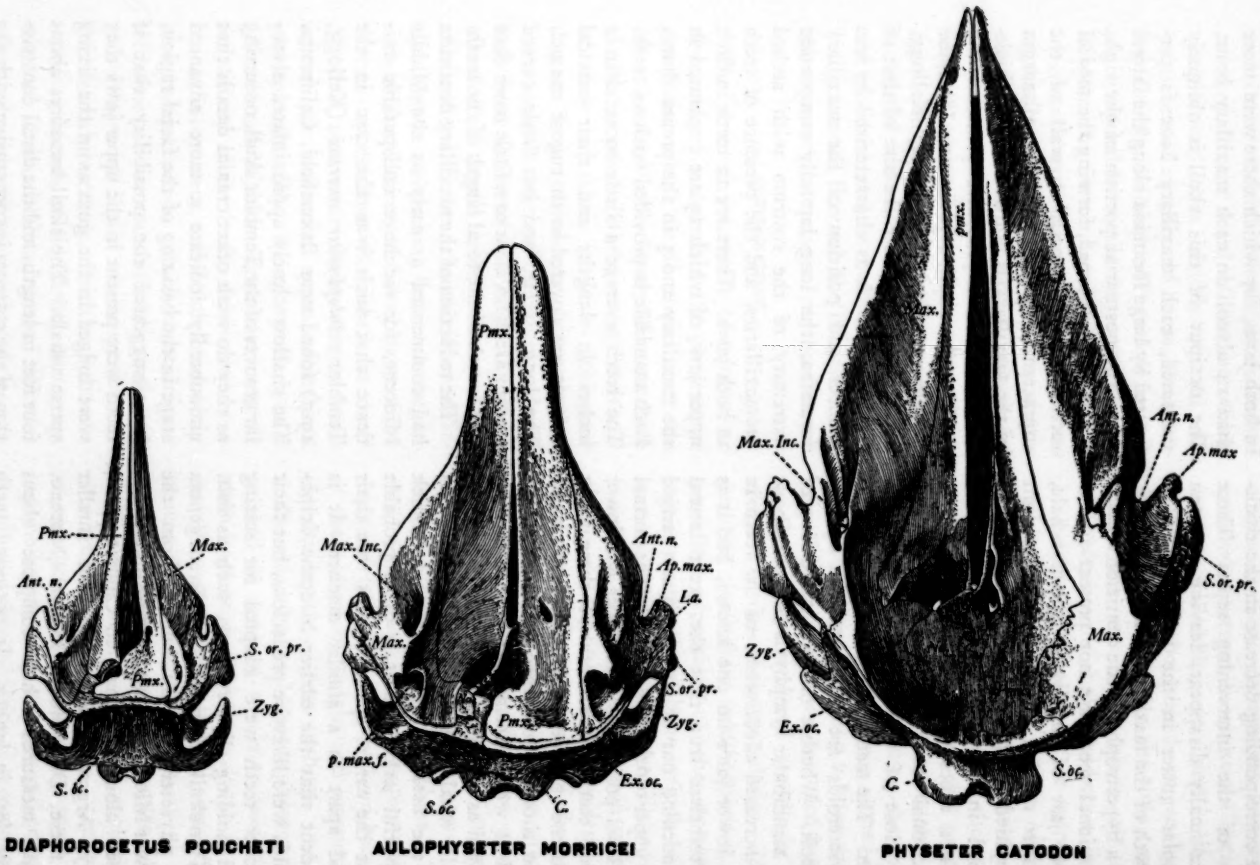


FIG. 14. DORSAL VIEWS OF SKULLS

Diaphorocetus poucheti, Lower Miocene, Patagonia. *Aulophyseter morricei*, Middle Miocene, California. *Physeter catodon*, Tasmania, young male (after Flower).

shallow alveolar grooves. There is a large incisure and a smaller posterior foramen in each maxillary bone above the orbit.

Vastness of size is so generally associated in the popular idea with the whalebone whales that relatively few realize that gigantic species have been developed also among the toothed whales. Both giants and dwarfs may appear in whales constructed along similar lines. The living sperm whale, or cachalot, *Physeter catodon*, is the largest known odontocete, either living or extinct, and there is only one described Miocene species *Ontocetus oxymycterus* (Kellogg, 1925) that approaches it in the size of the skull. Comparative measurements indicate that a complete skull of this extinct physeteroid would measure more than 12 feet in length. The extremity of the rostrum was formed by the premaxillaries, and three large teeth were implanted in each. The largest mandibular teeth measure about 12 inches in length, and all of the teeth in both jaws were lodged in distinct alveoli. It should be noted, however, that the alveoli were too large and the roots too loosely fitted to hold the teeth in position independently of a dense ligamentous gum. The enamel on the crowns of these teeth is ornamented with coarse longitudinal striae.

Physeteroids with functional teeth in the upper jaws continued to near the end of the Miocene, when they seem to have disappeared from geological history. Their remains have been found in Upper Miocene deposits in Europe, North America, and Japan. The incomplete skull of *Orycterocetus mediatlanticus* (Cope, 1895; Kellogg, 1925) found in the St. Mary's formation at Drum Point, Maryland, has the lateral margin of the maxillary excessively thickened at the level of the orbit, but the positions of the maxillary foramina and the disposition of the maxillary alveoli are similar to the Lower Miocene *Idiorophus*.

The number of physeteroid types (Abel, 1905) found in the Upper Miocene black crag of the Antwerp basin, Belgium, is truly surprising in view of their scarcity in later geological formations. The distinguished Austrian palaeontologist, Professor O. Abel has recognized a rather large number of physeteroids in these deposits, including *Scaldicetus mortezelensis*, *Physeterula dubusii*, *Thalassocetus antwerpiensis*, *Placoziphius duboisii*, and *Prophyseter dolloi*. The skulls of these extinct Belgian physeteroids differ from one another in certain details of cranial construction, but all possess the large supracranial basin. The largest of these is *Physeterula dubusii*, whose skull measures less than six feet in length; each mandibular ramus is furnished with 20 teeth about 5 inches long, of which 12 are restricted to the symphysis. No enamel is present on the crowns of these teeth. The other species have somewhat smaller skulls, those of *Scaldicetus mortezelensis* and *Placoziphius duboisii* being less than 3 feet in length. In *Placoziphius* the upper teeth seem to have been completely lost, for the alveolar grooves are nearly closed. *Scaldicetus* on the other hand is said to have retained the maxillary and premaxillary teeth, and the unworn teeth of this physeteroid have the crowns covered with longitudinally striated enamel, in addition to vestigial crenelated cutting edges. The roots of these teeth are simple and have a rather large pulp cavity.

The culmination of the tendency toward the abnormal development of a spermaceti cushion may be observed in the living genus *Physeter*, the great size of whose skull is disproportionate, in respect both to the brain and to the body. In this genus, the spermaceti cushion has attained

FIG. 14. DORSAL VIEWS OF SKULLS

Diaphorocetus poucheti, Lower Miocene, Patagonia. *Aulophyseter morricei*, Middle Miocene, California. *Physeter catodon*, Tasmania, young male (after Flower).

an enormous size, and in correlation with this increase the bones comprising the rostrum have expanded horizontally. In life the disproportionately large head abruptly truncated in front, small eyes placed near the angle of the mouth, and blowhole on the edge of the muzzle, in conjunction with a dorsal hump give *Physeter catodon* a very unusual appearance. Skulls of adults measure 16 feet or more in length and have a continuous maxillary alveolar groove without any indication of septa. The large palatine bones do not form any part of the backward sloping narial passages, and are overridden posteriorly and mesially by the pterygoid bones. As many as 27 teeth are lodged in each mandible, and the symphysis is equivalent to half of either ramus. The posterior margin of the supracranial depression is more abruptly elevated in the physeteroids than in any other family of cetaceans, and the basin extends farther forward. In general the physeteroid skull may be defined as having the rostrum longer than the cranium, no sagittal crest, rise of anterior border of lateral wall of supracranial basin within the antorbital notch, small lachrymals, elongated jugals with styliform processes, expanded palatines, small pterygoids, and large foramina, which connect with the infraorbital system.

KOGIIDAE

It is not improbable that, when more is known of the immediate predecessors of the living odontocetes, the diminutive living *Kogia breviceps* will be found an offshoot of some early Tertiary physeteroid. At present we have no knowledge of their previous geological history. Compared with a sixty-foot cachalot, an eleven-foot pigmy sperm whale seems rather small. It has an attenuated snout, eyes placed nearer to the forehead, blowholes on the forehead, and a falcate dorsal fin. The skull of this porpoise is characterized by a short rostrum, a well defined sagittal crest, rise of anterior border of lateral crest of supracranial basin outside of antorbital notches, large thickened lachrymal fused with styliform jugal, small palatines, expanded pterygoids, and small foramina connected with the infraorbital system. The mandible has a short symphysis and is furnished with 14 or 15 teeth.

POSSIBLE ANCESTORS OF THE MYSTICETI

The least modified cetacean skull thus far collected is represented by *Archaeodelphis patrius* (Allen, 1921), whose critical peculiarities of detail agree more closely with mysticete than with odontocete cranial construction. Annectant types are lacking to connect *Archaeodelphis* with any known cetothere, and the details hereinafter mentioned should not be interpreted as implying that this Eocene cetacean was the source to which cetotheres of later geological stages owed their origin. The most that can be said is that *Archaeodelphis* and the cetotheres are derivatives of the same common stock.

Structurally this skull is much less modified than any known fossil or living whalebone whale. Obvious peculiarities of the *Archaeodelphis* skull are the large orbit, elongate flattened nasals and extremities of premaxillaries situated almost entirely anterior to the supraorbital processes of the frontals, long and forward sloping narial passages with distinct dorsal nasal cavities, broad intertemporal region, a triangular lachrymal extending laterally as far as or beyond the maxillary and overspread by the latter, and a maxillary with infraorbital and ascending processes. The position of the maxillary with respect to the lachrymal, the orbit, and the supraorbital process of the frontal

may be regarded as an early stage in the development of conditions like those now seen in the mysticetes. The maxillary has an infraorbital process that projects backward to the level of the optic canal, and the ascending process has not been pushed backward very far over the upper surface of the supraorbital process of the frontal. In its essential features this bone is typically the interlocking sort of maxillary found in all known whalebone whale skulls. A subsequent constriction of the ascending process of the maxillary would lead to the presence of pterygoid fossae for accessory air sinuses of the inner ear and a backward infraorbital extension of the maxillary are prerequisites for any precursor of the mysticetes. The presence or absence of teeth on the rostrum, which is unknown, while interesting is of relatively little importance, for embryology shows us that the predecessors of the mysticetes were toothed whales. In another important detail, this skull resembles those of whalebone whales, for it has a periotic bone with a long apophysis wedged in between the exoccipital and the squamosal.

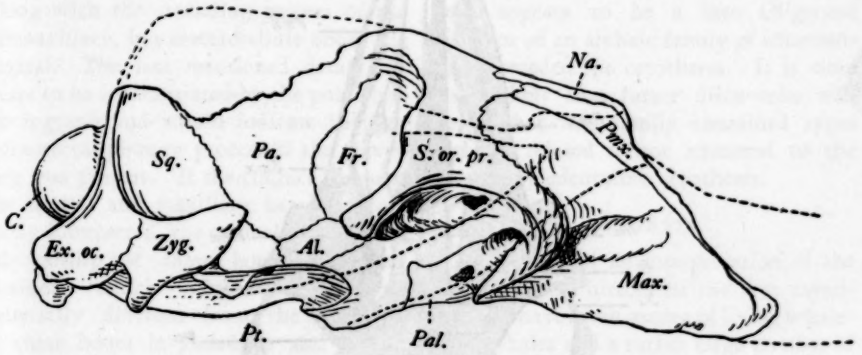


FIG. 15. LATERAL VIEW OF ARCHAEODELPHIS PATRIUS, UPPER EOCENE
Dotted lines indicate course of narial passages, narial cavity, and olfactory foramina

mysticete type of construction. The base of the ethmoid and the dorsal nasal cavities are roofed over by the nasal bones, and the palatine bones do not enter into the composition of the anterior walls of the narial passages, thus agreeing with the type of structure present in the mysticetes. The upper portion of the supraoccipital shield is destroyed, but it is evident that it has not extended forward far enough to meet the frontal. The parietals therefore form the vertex of the braincase. This skull has rather large pterygoid fossae, which agree in shape and position with those of mysticetes. The

At least one survivor, *Patriocetus*, of the archaic toothed whales has been found in the Aquitanian white sands of the Linz basin in Austria, along with *Cetotheriopsis*, the oldest known member of a family of primitive whalebone whales, the *Cetotheriidae*, and *Agriocetus*, whose exact relationships are still imperfectly known. The imperfect type skull and another fairly well preserved skull form the basis for *Patriocetus grateloupii*, which was thought by Professor Abel (1913) to be a precursor of the Mysticeti, but both are so coated with grains of sand that the sutures are obscured.

Whether *Patriocetus* belongs with the archaic toothed whales or whether it represents a precursor of the mysticetes are questions that have occasioned some difference of opinion. The deductions of Professor Abel and others on the mysticete relationships of *Patriocetus* are of little or no consequence in so far as the actual shape of the braincase is similar to *Archaeodelphis* and *Agorophius*. The most obvious peculiarity of the braincase of *Patriocetus* is the thin ledge-like projection from the parietal that extends backward from the supraorbital process to the supraoccipital and overhangs the temporal fossa.

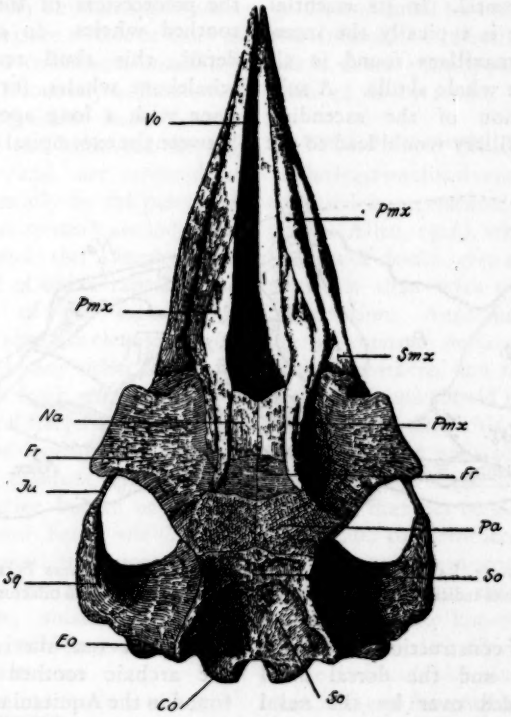


FIG. 16. DORSAL VIEW OF SKULL OF PATRIOCETUS GRATELOUPII, UPPER OLIGOCENE, LINZ, AUSTRIA
(After Abel)

precursor of the whalebone whales is concerned, for this cetacean was contemporaneous with at least one member of that group. The question to be settled, if possible, is whether or not the mysticetes passed through a stage of cranial architecture comparable to the restorations given by Abel. The published photographs indicate that the general

Several details of the restorations and description given by Abel are so contrary to probability that they must await confirmation by the discovery of a much better preserved skull. These questions of detail, if confirmed, will indicate the existence of another unexplained factor in the telescoping process. On the restorations of the skull, the maxillary is not

fastened to the braincase, but is represented as stopping at the level of the anterior margin of the frontal, with no part of this bone extending backward above the supraorbital process. According to this interpretation the rostrum was supported solely by the vomer and the ascending processes of the premaxillaries, which extend backward to the parietals, a mechanical arrangement that is not only improbable, but structurally defective. Professor Abel states that the posterointernal extremity of the maxillary stops at the antorbital line and does not push backward across the supraorbital process along with the ascending process of the premaxillary, but instead slides under the frontal. The last mentioned detail appears to be substantiated by the published photograph and would indicate that an infraorbital plate or process of the maxillary was present. If the contact between the frontal and maxillary has been correctly interpreted, the normal mammalian relationship of these bones has been retained, which furthermore is not materially different from the relations of these bones in *Eubalaena* and in the zeuglodont type of skull. Granting that the restoration represents the actual present condition of the specimen, there is no reason why the supraorbital process may not have been narrowly margined anteriorly by a thin plate of the posterior end of the maxillary, which was destroyed without leaving any trace, if the connection between these elements was so loose that no impression was made on the upper surface of the frontal. According to König (1911), who was the first to comment on this skull, its characters were not very different from those of *Agorophius*, on which the maxillary does overspread the supraorbital process. This observation is disputed by Professor Abel (1924). *Xenorophus* and *Rhachianectes* are the only known cetaceans in which it is apparent that the maxillary does not reach posterointernally as far back as the premaxillary, but on both of these skulls the maxillary has been thrust backward over the frontal. It is stated that the lachrymal can be seen from a ventral view in the antorbital notch, but this bone is not so indicated on any of the restorations. The dentition is still functional in *Patriocetus*, and the braincase is not materially unlike those of generalized toothed whales, but the periotic bone is of the mysticete type, with long apophysis wedged in between the exoccipital and squamosal. *Patriocetus* appears to be a late Oligocene survivor of an archaic family of cetaceans that preceded the cetotheres. It is more than likely that future discoveries will show that this family contained types directly related if not ancestral to the succeeding edentulous cetotheres.

MYSTICETI

As a basis for an interpretation of the developmental history of the true mysticetes we have seven genera of living whalebone whales and a rather large number of fossil species ranging in age from Upper Oligocene to and including the Pleistocene. Many of them, however, are based on very scanty remains. Starting with the more generalized cetacean skull on one hand and ending with the modernized mysticete on the other, it becomes apparent that the possibilities for remodeling are limited to certain definite details and that the fossil types represent successive stages in the developmental history of several phyla. If we based our deductions solely on a critical comparison of the Austrian Upper Oligocene and the Patagonian Lower Miocene mysticete skulls, we should be led to assume that the forward overthrust of the posterior occipital elements had precedence over the

backward interdigitation of the median rostral elements. Nevertheless, skulls of Miocene cetotheres from later geological stages do not lend any support to this assumption, for *Cetotherium* and related genera exhibit a less advanced stage in the forward overthrust of posterior occipital elements and a pronounced interdigitation of rostral and cranial elements. It is obvious that our available material is too meagre for more than vague generalization on the lines of descent and that any discussion of the history of the mysticetes must be confined to types arbitrarily selected to illustrate certain features of this general evolutionary process. There is evidence that several phyla of cetotheres advanced along similar lines. In one direction there is a persistence of the dominant forward overthrust of posterior occipital elements, and an absence of rostral and cranial interdigitation. This is the type of remodeling that led up to the modernized balaenids. In the other direction, the forward overthrust of the posterior occipital elements was coupled with a backward interdigitation of the median rostral elements, as a result of which the posterointernal extremities of the maxillaries, the premaxillaries, and the nasal bones became suturally united with the frontals on the vertex of the interorbital region. Some of the extinct cetotheres and all of the living balaenopterine whales exhibit this type of telescoping. Various intermediate stages of these two general trends occur among the cetotheres.

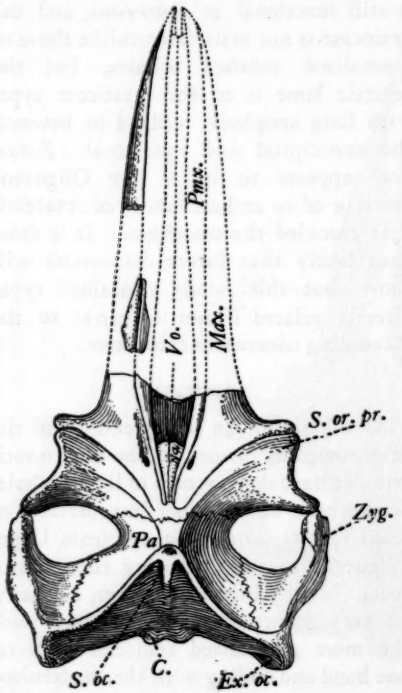


FIG. 17. DORSAL VIEW OF SKULL OF CETOTHERIUM RATHKII, UPPER MIOCENE, RUSSIA
(After Brandt)

BALAENIDAE

Winge (1918) was the first to suggest that the balaenids represent the most primitive known mysticetes, although at the time this was written no right whales older than Pliocene had been described. That the Balaenidae were already differentiated as a family before the Lower Miocene is made certain by the occurrence of an already specialized form, *Morenocetus parvus* (Cabrera, 1926), in the Patagonian marine formation of Chubut, Argentine Republic. The dominant forward overthrust of the posterior cranial elements has carried the apex of the supraoccipital shield to the anterior interorbital region, excluding the parietals from the vertex of the skull, and reducing the median exposure of the frontals to a narrow strip behind the nasal bones. The sutures show that the nasal bones, the premaxillaries, and the maxillaries occupied the usual balaenid position

anterior to the supraorbital processes. The latter slant backwards and slope from the interorbital region to the rim of the orbit. The subsequent developmental history of this family during the Miocene is unknown. Several types of more highly specialized balaenids such as *Balaenula balaenopsis* (Van Beneden, 1878) make their appearance during the Pliocene, and their successors are the living genera that comprise the family Balaenidae.

NEOBALAENIDAE

In the progressive specialization and differentiation of the balaenid stock, two or more trends of development were followed, one of which resulted in the elongation and lateral compression of the rostrum as seen in the Balaenidae and the other by a retention with very little modification of the early cetothere type of rostrum. The living pigmy whale (*Neobalaena marginata*) belongs to the latter group. The rostrum of this whale is very little longer than the occipital shield and tapers rapidly from a broad base to a slender tip. The mandible is unusually robust and is strongly bowed outward. The skeleton of this whale has more peculiarities than any other living mysticete. It has 17 pairs of large broad ribs, of which at least eight are not articulated. The seven cervicals are completely fused with one another. There are 18 dorsal vertebrae, but no ribs are attached to the first of the series. The lumbar vertebrae have been reduced to one or two, and the caudals do not exceed 14 in number. Future discoveries of fossil mysticetes in the New Zealand and Australian region should throw much light on the developmental history of *Neobalaena*, which seems to be an offshoot of some early stock that passed through its development in the Southern Hemisphere, following a somewhat different path from the balaenids, and acquired peculiarities in the form of the ribs, the vertebral column, and the hand.

CETOTHERIIDAE

If we take their features seriatim, we find that the skulls of all known edentulous Miocene cetotheres have supraorbital processes that slope gradually outward from the dorsal surface of the interorbital region to the rim of the orbit and are never abruptly depressed basally below the level of the former as in the balaenopterine whales. Many of these cetotheres retained a well defined intertemporal region, constituted entirely by the parietals, which meet along the median line in front of the supraoccipital shield. In most species the braincase is short and broad, but the supraoccipital shield is quite variable in shape and extent, depending in part upon the degree of forward overthrust. The narrow ascending process of the maxillary is suturally united with the mesial projection of the frontal. The general arrangement of the bones that inclose the narial passages is more nearly in agreement with the typical structure of terrestrial mammals than with the toothed whales. The nasal bones and mesial projections of the frontals completely roof over the ethmoid region and the dorsal nasal cavity, and in addition the palatine is excluded from the anterior wall of the corresponding narial passage. The choanae lie behind the anterior opening leading to the nostrils, and the infraorbital plate of the maxillary is retained.

The skull of the Upper Oligocene *Cetotheriopsis lintianus* (Meyer, 1849; Brandt, 1873), found near Linz in Austria, is characterized in part by a high narrow triangular supraoccipital shield, which curves more forward than upward and is divided mesially by a long vertical

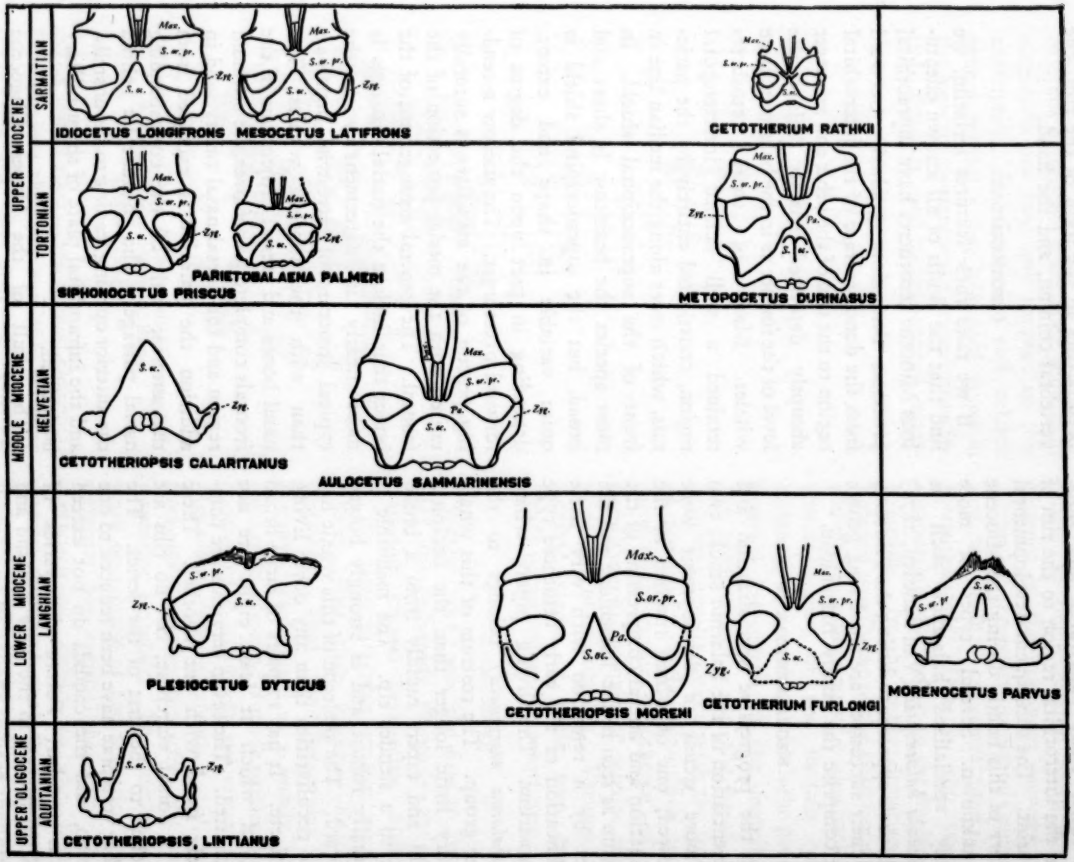


FIG. 18. DIAGRAM ILLUSTRATING STAGES OF TELESCOPING IN EXISTENCE DURING THE MIOCENE IN THE FAMILIES CETOTHERIIDAE AND BALAENIDAE

carina; elongate zygomatic processes, which do not reach forward to the level of the apex of the supraoccipital shield; and the vertex of the braincase as viewed from behind is strongly depressed below the arching lambdoid crests. This imperfect cetothere skull is quite important, for it demonstrates that telescoping was an accomplished fact by the close of the Oligocene and that an advanced stage in the forward thrust of posterior occipital elements, such as is found in *Cetotheriopsis*, must have been preceded by developmental stages that led up to this type of telescoping. The Oligocene period unquestionably witnessed great elaboration of the telescoping process in the cetotheres, but unfortunately their known fossil remains are so scant that they give us no clew as to how this extraordinary condition came about. The scarcity of fossil cetaceans in Oligocene formations seems all the more surprising in view of the wide variety of types that make their appearance in formations of Lower Miocene age.

Two distinct types of cetothere skulls from the Lower Miocene Patagonian marine formation of Chubut Territory, Argentine Republic, have been obtained. One of these, *Cetotheriopsis moreni* (Lydekker, 1894), consists of a skull measuring 74 inches in length, a mandible, tympanic bullae, and vertebrae. Though originally assigned to the genus *Cetotherium* it is obvious that this allocation is incorrect, as is evidenced by the absence of anterior temporal crests, the extreme flatness of the cranium, the triangular supraoccipital shield extending forward beyond the level of the posterior margins of the supraorbital processes, the very broad maxillaries, and the elongated nasal bones situated almost entirely anterior to the preorbital angles of the supraorbital processes. This cetothere is tentatively referred to the genus *Cetotheriopsis* on account of obvious similarities in the development and extent of the supraoccipital shield. Cetothere skulls with supraoccipital shields of similar proportions also occur in more recent geological stages.

The other Patagonian skull "*Plesiocetus*" *dyticus* (Cabrera, 1926) exhibits a second type of occipital shield. The inclination of the supraorbital processes appears rather unusual at first sight, but this abnormality is largely the result of distortion from rock pressure. The supraoccipital shield is distinctly constricted near the apex. As compared with *Cetotheriopsis moreni* the braincase is narrower at the base, the shield is more rounded, and the lambdoid crests are more salient, but the vertex is depressed as in the former. The forward movement of the supraoccipital pushed the parietals in front of it, so that they overspread the posterior borders of the frontals in the interorbital region. The sutures on the anterior borders of the frontals indicate that the nasal bones and the median rostral elements were slightly interdigitated with the cranium. The extent of the forward overthrust of the supraoccipital shield and the backward interdigitation of the mesial portion of the rostrum, the unusually slender supraorbital processes, the position of the nasal bones, as well as the relations of the bones in the intertemporal region show that this cetothere represents another advanced stage in the telescoping of the mysticete skull.

In one or more phyla of mysticetes the telescoping of the skull seems to have been largely limited to a forward movement of the posterior cranial elements, for the interdigitation of the rostral and cranial elements is very slight. This condition prevails in skulls of the Helvetian "*Mesocetus*" *hungaricus* (Kadic, 1907)

FIG. 18. DIAGRAM ILLUSTRATING STAGES OF TELESCOPING IN EXISTENCE DURING THE MIOCENE IN THE FAMILIES CETOTHERIIDAE AND BALAENIDAE

and the Tortonian *Siphonocetus priscus*, and *Parietobalaena palmeri* (Kellogg, 1924), on which the nasal bones, the premaxillaries, and the rudimentary postero-internal extremities of the maxillaries, while suturally united with the mesial projections of the frontals, are situated for the most part anterior to the level of the preorbital angles of the supraorbital processes. The apex of the supraoccipital shield extends forward beyond the extremities of the zygomatic processes and the posterior margins of the supraorbital processes. The frontals are broadly exposed in the interorbital region, and the parietals are shoved forward across the frontals, meeting on the mid-line to form a short sagittal crest.

The interdigitation of the rostral and cranial portions of the skull, in so far as substantiated by described specimens, is first observed in the Lower Miocene "*Cetotherium*" *furlongi* (Kellogg, 1925), which was found in Monterey County, California. The backward interdigitation of the mesial portion of the rostrum carried the ascending processes of the maxillaries and the premaxillaries, as well as the nasal bones, beyond the level of the preorbital angles of the supraorbital processes. In consequence of this backward movement, the facial portion of the skull becomes "dished in" mesially in some of the succeeding cetotheres, the anterior borders of the supraorbital processes curving forward and outward. The Tortonian *Cephalotropis coronatus* (Case, 1904), the Anversian *Mesocetus longirostris* (Van Beneden, 1886), and the Sarmatian *Cetotherium rathkii* (Brandt, 1873), and *Cetotherium helmersenii* may be cited as examples of this stage in the telescoping process. Some of these species were no larger than the new-born young of living finbacks.

Skulls of species referable to the Miocene genus *Cetotherium* were characterized in part by forward curving supraorbital processes, by the facial position of the nasal bones, by anteriorly directed zygomatic processes with peculiar elongated glenoid articular surfaces, as well as by long slender mandibles. A peculiarity that distinguished *Cetotherium* and related genera from other Miocene cetotheres is the presence of a sharply defined anterior temporal crest, which seems to foreshadow the abrupt depression of the basal portion of the supraorbital process seen in balaenopterine whales. Cetotheres belonging to this small group likewise possess the least modified braincase, for the parietals come in contact with each other in the intertemporal region, and the apex of the supraoccipital shield lies behind the level of the supraorbital processes.

The interdigitation of the rostral and cranial elements is well marked in a mysticete from Monte Titano, San Marino, Italy, which Capellini (1901) named "*Aulocetus*" *sammarinensis*. The formation from which this specimen was obtained has been allocated by some geologists to the Langhian stage and by others to the Helvetian. The narrow nasal bones have not been shortened, although they lie almost entirely behind the level of the preorbital angles of the supraorbital processes of the frontals, and are as long as or longer than the breadth of the extremities of the latter. A short intertemporal region with broad sagittal crest is retained, and the apex of the rounded supraoccipital shield is not extended forward to the level of the extremities of the outward bowed zygomatic processes.

In the preceding brief résumé of the cetotheres the writer has endeavored to select types that show the main structural features of their evolutionary history, and many equally important species have been omitted. Capellini, Strobel, Portis,

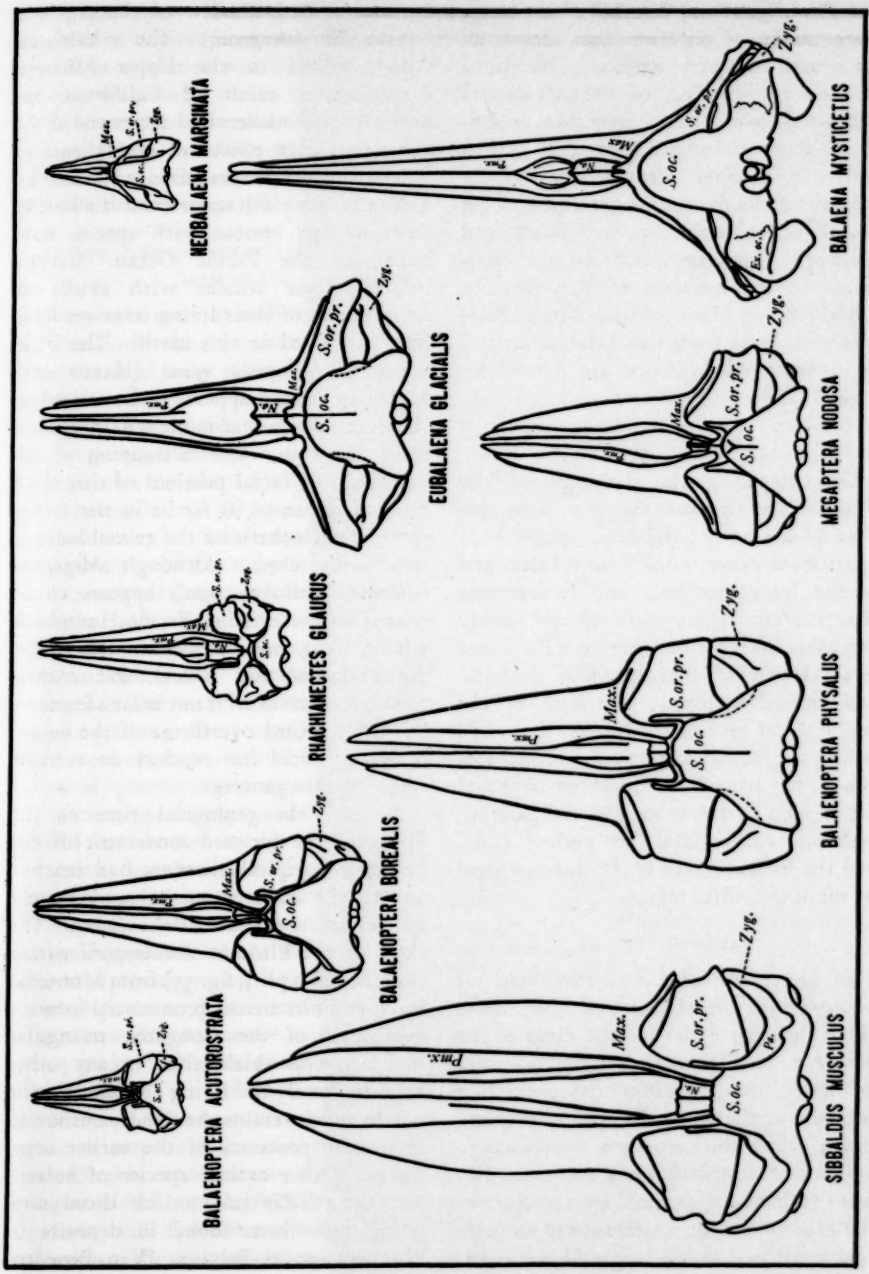


FIG. 19. DIAGRAM ILLUSTRATING STAGES OF TELESCOPING REPRESENTED AMONG LIVING MYSTICETI

and Brandt have figured and described a rather large number of cetotheres from Italy and southern Russia. Conditions for the preservation of the mysticetes apparently were more favorable in Belgium than elsewhere, for the largest faunas of extinct cetotheres of Upper Miocene and Lower Pliocene age thus far known occur in the Antwerp Basin, and these species are exceptionally well illustrated in the memoirs of Van Beneden (1885–1886). Many of the Upper Miocene cetotheres from the Atlantic coastal plain described by Cope are figured by Case (1904).

RHACHIANECTIDAE

On comparing the diagrams of the skulls of living mysticetes it will be seen that *Rhachianectes* (Andrews, 1914) stands apart from other whalebone whales, and is the least modified, and furthermore that the conditions observed are readily derivable from the cetothere skull. There is a well marked interdigitation of rostral and cranial elements, the base of the supraorbital process is abruptly depressed below the dorsal level, the overthrust of the supraoccipital shield has not advanced far enough to eliminate the interparietal, although the parietals are pushed apart, and the frontal bones are broadly exposed in the interorbital region.

BALAENOPTERIDAE

In North America and elsewhere we observe that the modernized types make their appearance toward the close of the Miocene, and that the Upper Miocene witnessed the reduction and extinction of many of the types that preceded them. For a while the cetotheres continued to exist in diminished numbers, but they seem to have disappeared by the close of the Pliocene. The appearance of modernized mysticetes in the Upper Miocene was not unexpected in view of the previous history of the group. The whalebone whales found in the Upper Miocene diatomaceous earth of California are unmistakably modernized types and show the cumulative effects of specialization. All of the mysticetes obtained from the diatomaceous earth series exhibit affinities more or less remote with species now living in the Pacific Ocean. Extinct balaenopterine whales with skulls as large as any of their living relatives have been excavated in this earth. The little finner, *Balaenoptera ryani* (Hanna and McLellan, 1924), appears to be related to the living sharp-head finner whale, *Balaenoptera davidsoni*. The telescoping of the occipital and facial portions of this skull has not advanced as far as in the living species, but otherwise the resemblance is remarkably close. Although *Megaptera miocaena* (Kellogg, 1922) appears to be related to the existing Pacific Humpback whale, *Megaptera versabilis*, the interdigitation of the rostral and cranial elements of the skull is not as far advanced, but the forward overthrust of the supraoccipital shield has reached an extreme stage in this process.

As early in geological time as the Pliocene, the forward movement of the posterior occipital elements had reached an extreme stage in one or more extinct species of the genus *Balaenoptera*. The skull of the Pliocene *Balaenoptera cortesii* (Portis, 1885, pl. 3, fig. 35) from Montafia, Italy, exhibits a more pronounced forward overthrust of the elongated triangular supraoccipital shield than in any other known fossil or living balaenopterine whale, but it retains the slender outbowed zygomatic processes of the earlier cetotheres. Other extinct species of balaenopterine whales not unlike those now living have been found in deposits of Pliocene age in Belgium (Van Beneden,

1882) and Italy (Portis, 1885). One of the most complete Pliocene balaenopterine skulls in existence was found in 1806 on Monte Pulgnasco, Italy, in blue clay of of Plaisancian age and it, *Balaenoptera cuvieri* (Van Beneden, 1875), bears the name of the famous French palaeontologist, Baron Georges Cuvier.

MORPHOLOGICAL PECULIARITIES OF THE MYSTICETES

In spite of the extraordinary remodeling of the skull, the mysticetes (True, 1904) have retained many primitive features that are no longer found in odontocetes. The relations of the bones in the region of the narial passages are essentially normal, and the choanae lie behind the opening leading to the blow holes. The proximal ethmoid region and the dorsal nasal cavity are completely roofed over by the nasal bones. A separate lachrymal bone is retained, but the lachrymal duct has disappeared. The palatine is excluded from the anterior wall of the narial passage. It has increased in size and has been forced backward, pushing the pterygoid behind it. The most extreme stage of the mysticete type of telescoping is seen in *Sibbaldus*, in which the forward overthrust of the shield has carried the apex of the supraoccipital to the nasal bones, and the parietal sends forward a thin plate, which is applied to the lateral surface of the ascending process of the maxillary above the abruptly depressed base of the supraorbital process. The interlocking of the rostrum with the cranium is more obvious than in any other balaenopterine whale. In *Neobalaena* and *Balaena* the forward overthrust of the supraoccipital shield has gone a step further, and its apex lies considerably anterior to the preorbital angles of the supraorbital processes. In *Balaena* and *Eubalaena* the lateral compression of the rostrum is very conspicuous. A pterygoid fossa for an accessory air sinus has been formed in front of the inner ear. The balaenid and balaenopterine whales have a similar type of scapula, with large functional acromion and coracoid processes. These processes are reduced to mere tubercles in the scapula of *Megaptera*. The primitive condition of the elbow and wrist joints has been lost. The carpus in *Balaena* is immovable and broad, and conspicuously lengthened in *Megaptera*. The lumbar vertebrae are furnished with widely projecting transverse processes. The ribs exhibit a tendency to restrict their connexion with the thoracic vertebrae and with the atrophied sternum, which consists of the manubrium alone. The ribs of living mysticetes are single-headed in contrast to the normal type of rib found in some of the cetotheres. Considerable remnants of the hind limb are retained, including the rod-like pelvis, the atrophied femur, and in some cases a vestige of the upper end of the tibia. The caudal vertebrae acquire large centra with broad flattened transverse processes to conform to the manner in which the tail is wielded.

We have seen that the early cetotheres lost their teeth and acquired two rows of blade-like plates of baleen depending from the roof of the mouth, which served as a seine when the animal was feeding. Small crustaceans or fish constitute the food of the living whalebone whales, and the cetotheres no doubt subsisted on the same types of food. In the living mysticetes the prey is engulfed in the oral cavity along with a large quantity of water, which necessarily must be expelled by the tongue before such small prey can be swallowed. Hence these plates of baleen with internal marginal fringes of intermatted bristle-like fibers form a strainer remarkably well adapted for

taking surface-swimming crustaceans or for impounding small fish, which are scooped up by the animal when plunging forward with mouth open. The capacity of the mouth was increased in two ways. In the balaenids it has been accomplished by arching the upper jaws and in the others by a bowing outward of the lower jaws in conjunction with a broadening of the rostrum. Surprising as it may seem four barrels of shrimps were taken from the partially filled stomach of a huge blue whale (Andrews, 1916), whose throat measured about 9 inches in diameter.

It is worth while then to explain just what has been accomplished by the remodeling of the generalized mysticete skull. This brings us around again to a comparison of living and extinct types. In general it may be stated that the forward movement and expansion of the supraoccipital shield was followed or accompanied by a broadening of the base of the skull. This forward overthrust of the posterior occipital elements also changed the relative positions of the zygomatic processes, for they become more robust and their articular surfaces come to lie near the level of the occipital condyles. The mouth cavity increased in size, and this in turn permitted a lengthening and expansion of the blades of baleen that hang from the roof of the mouth. The mandibles acquired a disproportionately large size in comparison with the braincase, becoming bowed outward and loosely connected anteriorly. The symphysis disappeared, and the ligaments that bind the articular head of the mandible to the glenoid articular surface developed the strength necessary to bear the great weight of the outbowing lower jaws. The opening leading to the nostrils or "blow holes" was drawn backward in proximity with the anterior wall of the braincase. The posterior position of the blow-holes permitted exhalation and inhalation without elevation of the muzzle above the water level, which was rendered difficult, if not impossible, by reason of the inflexibility of the neck. The increase in the size and proportions of the skull, the outbowing of the lower jaws, and the development of long blades of baleen attached to the roof of the mouth, required a firm socket to support the enormous increase in the weight of the head suspended from it. This result could be secured by the development of massive cervicals, or by the shortening of the neck and by the ultimate fusion of the seven cervicals into a compact mass as in *Balaena mysticetus* and *Eubalaena glacialis*. The ankylosis of the cervical vertebrae and their fusion into a compact immovable mass is believed to be the culmination of this evolutionary trend. In the case of any pelagic mammal having feeding habits similar to those of the whalebone whales, flexibility of the neck would be a mechanical weakness; hence the short neck appears to fulfill the necessary requirements for cetaceans with relatively large skulls. The basicranial region was largely protected from telescoping by the relations of the maxillary and frontal, and consequently the nasal cavity retains a cribriform plate with passages for the olfactory nerves as well as remnants of the turbinated bones, including the ethmoturbinals.

It must be understood that this summary attempts to account merely for the general features of the evolutionary history of the mysticetes, and that a late stage in this process may appear at an early geological time or an early stage may persist to the present day. The skull of the living gray whale (*Rhachianectes glaucus*) is constructed along the lines of an early stage and has been called a living fossil. Conversely the skull of the Lower Miocene *Morenocetus parvus* has already acquired

many peculiarities of detail that represent a late stage of the telescoping process.

Recent studies by Ridewood (1922) on embryo skulls of highly telescoped mysticetes confirm in a large measure the general features of the palaeontological evidence. Skulls of embryos exhibit a rather broad intertemporal region formed by the parietal bones. An interparietal bone has been observed in the skull of a 9 inch foetus of *Balaenoptera acuto-rostrata* and in a foetus of *Balaenoptera borealis* measuring 3 feet 6 inches in length. No sign of an interparietal bone was observed in the skull of a foetus of *Sibbaldus musculus* measuring 6 feet 4 inches in length or in one of *Megaptera nodosa* measuring 27 inches in length. In all of the above mentioned embryo skulls, the parietal bones have been pushed forward across the frontals.

Embryology also furnishes the evidence that the progenitors of the mysticetes were provided with teeth. As many as 40 or even more minute teeth with pin-like crowns may be found hidden in the gum on the maxillary of a foetal mysticete, but they are soon resorbed. The atrophy of the teeth was followed by the growth of papillae (Tullberg, 1883) along the outer margin of the upper jaw, and these developed into a series of crosswise placed corneous blades, the baleen. An inquiry into the morphological features of the mysticetes leads one to the conclusion that many of the peculiarities of detail were adjustments to unexpected conditions associated with the procurement of food. An abundance of soft-bodied crustaceans provided ample and readily obtainable food, which required no mastication, but which did require some structure adapted for catching such minute prey. The blades of baleen are remarkably well adapted for this purpose, and the remodeling of the skull seems to have been profoundly influenced by their development.

ANATOMICAL AND PHYSIOLOGICAL ADJUSTMENTS

Adaptation to life in the water has brought about many changes, as already indicated, in the bodily organization of cetaceans. We observe that the motive power was transferred from the limbs, which originally served as ambulatory organs, to the hinder end of the body, resulting in the development of caudal flukes, which became the propelling mechanism; the hind limbs disappeared; and the fore limbs were modified into fin-like organs, which served as rudders. This adaptation is not a comparatively recent biological phenomenon, for a similar remodeling of the skeleton in a group of marine reptiles, the ichthyosaurs, took place at an earlier period in the earth's history. Convergent developments of independent origin such as these indicate that the remodeling of the skeleton was governed by the operation of some general principle of aquatic adaptation.

Flippers of whales bear little resemblance to the fore limbs of land mammals, for they are overlain with blubber and are fashioned like a paddle with margins hardened by fibro-cartilage. Nevertheless they are supported and constructed with similar bones, muscles, blood vessels, and nerves. The hand has been remodeled to conform to the use to which it is put. The wrist bones have lost their original shape and occasionally fuse into a compact mass in old individuals. There has been a reduplication of the bones in the fingers, which has been variously explained as the result of a secondary division of the strand of cartilage attached to the terminal phalanx, of intercalary syndesmoses, or of double epiphysis formation (Küken-

thal, 1891). In the typical mammalian hand the number of phalanges in each finger does not exceed three, whereas as many as seventeen have been observed in foetuses of *Globicephala*. Whalebone whales apparently lack the thumb, but it is present in the toothed whales. The chief function of the flippers is to enable the whale to descend or ascend, or to turn sideways. They are used mainly for steering and balancing, and have lost their former rowing function. The propelling mechanism of a whale is centered in the powerful flukes at the end of the tail, and the muscles and tendons that control these organs of propulsion act as levers, which pull them in an up and down direction. The greatest velocity is produced by alternate upward and downward strokes of the flukes. When proceeding at a slower speed the flukes cut the water laterally and obliquely downward.

Less striking physiological phenomena have been observed in the thermal adjustments. Since the capacity of water for conducting heat is 27 times as great as that of air, whales would lose a vast amount of body heat were it not for the presence of a blanket-like heat-retaining layer of fat over the whole body and the absence of sweat or sudoriferous glands. Whales in tropical waters need this protection nearly as much as those in temperate or cooler water, for the individual body temperatures of whales are higher than the water they frequent. The body temperature of the Sei whale (*Balaenoptera borealis*) is between 95° and 97°F., and that of the common harbor porpoise (*Phocaena phocoena*) is 96°F.

The hide of whales is endowed with certain histological and structural features that afford the maximum elasticity, and conversely are capable of retarding increasing compression on the thorax. The fibrous blubber has tremendous strength and tenacity, for it will resist a strain of several thousand pounds. Finbacks have been known to drag a ship when the prongs of the harpoon were merely caught under the blubber on the back.

Adjustments and modifications in the structures that function in the process of breathing were necessary to permit feeding below the surface. Water would surely get into the lungs during swimming with a wide open mouth were it not for the fact that a whale's narial passages do not open into the throat as in land mammals. A continuous tube between the narial passages and the trachea or windpipe is formed by an elongation of the arytenoid cartilages and the epiglottis, which fits into the soft palate. Other anatomical and physiological adjustments have come about to permit sustained submergence. Whales can remain submerged for varying lengths of time, as a rule from 7 to 15 minutes, but in case of necessity for 2 hours (Lillie, 1915). Prolonged submergence requires an adequate supply of oxygenated blood, but it is also true that the compression of the gases in the lungs would raise the partial pressure of the oxygen in the alveoli so that practically all of it could be consumed. Some provision has also been made for the absorption of the accumulated carbon dioxide.

The closing apparatus of the nose is equally interesting, for closure is accomplished in an entirely different manner in the two groups of living whales. The toothed whales have a single external nostril, while the whalebone whales have a double nostril. In the case of the toothed whales the narial cavity is divided into a series of pockets into which the narial passages open, and between these pockets are a series of plugs controlled by muscles that apparently contract when pressure is exerted on the

external flap of fibro-elastic cartilage that covers the external nostril. Returning to the whalebone whales we observe that the tubular narial passages slope forward and upward, and are furnished with spiral folds that fit into one another when pressure is exerted from without. Although the closing mechanism is constructed along different lines in the two groups, in both the nostrils are effectually closed when the animal is submerged.

VISUAL SENSE

Most whales have such acute powers of hearing that it is an open question whether they see or merely hear objects that attract their attention. Nevertheless we have indubitable evidence that the eyes of cetaceans are adjusted to the specific functions they have to perform. In its gross features the whale eye differs from that of a land mammal in having the eyeball immovable, eyelids without eyelashes, no tarsus or supporting cartilage in the eyelid, no Meibomian glands, and a downward direction of the eye axis. As a result of an aquatic mode of life whales have acquired a more spherical lens and a greatly thickened sclera. The ciliary processes and their muscles are reduced in size and have lost their original function of controlling the shape of the lens. The tension of the suspensory membrane (the *zonula zinnii*) is not great enough to flatten the anterior surface of the lens, and as a general rule the latter retains a more or less spherical shape. Whales thus lack the power of accommodation.

Since the functional irritant for the dioptrical or recipient apparatus of any mammal is light, to function correctly the eye must be constructed so that clear cut pictures are formed on any spot of the retina. Inasmuch as the refractive index of sea water is not the same as that of air, the eyes of whales must be adjusted to function when immersed. There is so little difference in the refractive indices of sea water and of the aqueous humor that the cornea is dioptrically inoperative when the eye is submerged, and the dioptric apparatus is thus reduced to the lens. To compensate for this (fig. 20, diagram 6), however, the curvatures of the anterior and posterior surfaces, as well as the axis or height of the lens and the refractive indices of the liquid media, have been corrected so that light rays passing through sea water are brought to a focus on the retina.

A number of investigators have pointed out that the eyes of many of our living land mammals do not possess the power of accommodation, and it is not unlikely that similar conditions prevailed among the animals of the past. Diagram 2 represents a normal or emmetropic eye, in which parallel rays of light reaching the eye through the air are brought to a focus on the retina. Now if a land mammal with an eye of this sort should be transferred to a pelagic habitat, its vision would be impaired, for only the outlines of objects viewed under water would be recognizable, because the light rays reaching the eye through sea water would be focussed beyond the retina (Diagram 3). Even with the maximum accommodation, in which the anterior and posterior surfaces of the lens have the same radius of curvature, parallel rays of light reaching the eye through sea water would be focussed beyond the retina. Unless the axis or height of the lens were increased and the refractive indices of the surrounding liquid media were altered slightly, the eye would function imperfectly when immersed in sea water.

Under atmospheric conditions the eyes of most whales are myopic, that is the

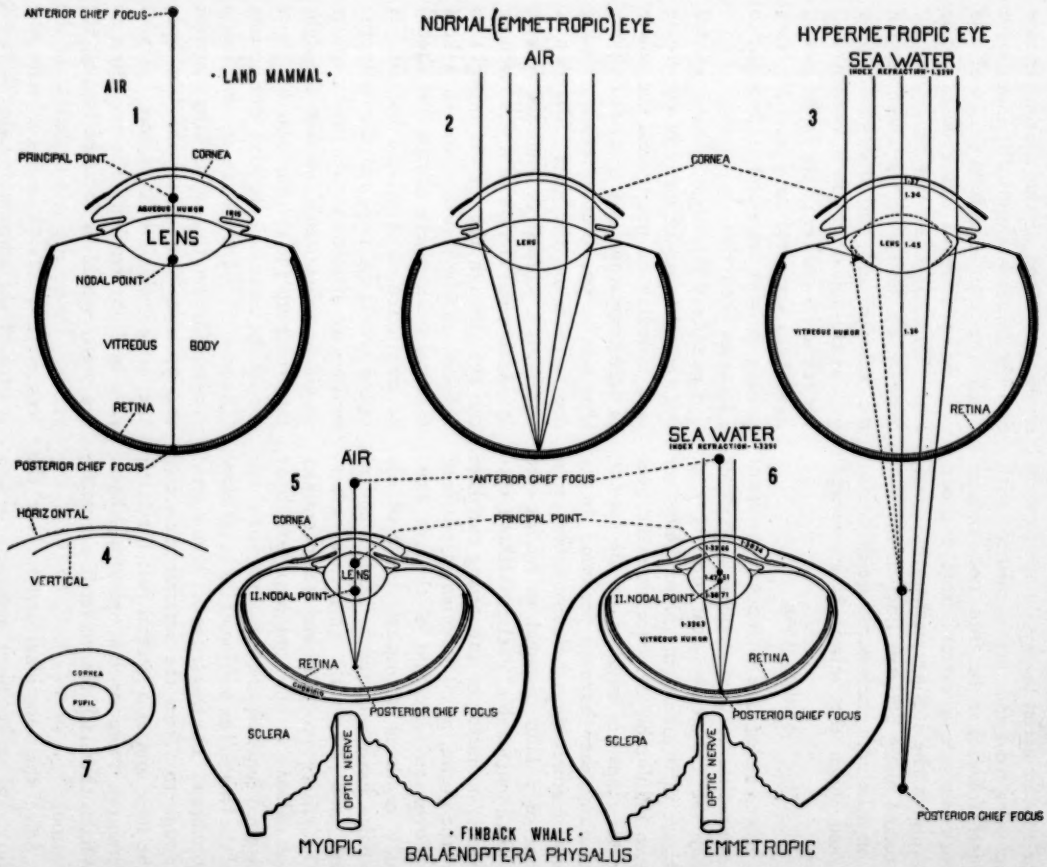


FIG. 20. DIAGRAMS SHOWING FOCAL POINTS OF PARALLEL RAYS OF LIGHT REACHING THE EYE THROUGH AIR AND THROUGH SEA WATER

light rays are brought to a focus in front of the retina. Thus when a whale tries to view objects above the water level (Diagram 5) it is troubled not only with astigmatism because of differences in curvature of the cornea in the two directions (Diagram 4), but also in being unable to change the curvature of the lens for optical accommodation because of defective ciliary muscles. According to Matthiessen (1886–93) the cornea of a whale living in salt water functions like a weak dispersive lens and, although the curvature of the cornea has little optical significance, an increase in size brings more light through the pupil to the peripheral parts. From an optical standpoint it would be to the advantage of a whale to have a large cornea, for they have to see with a weak light when feeding below the surface. The deeper a whale dives the weaker the light it has to see by. There may be some question, however, as to the limits of vision in the inky darkness that prevails in the depths of the sea. The bottlenosed beaked whale (*Hyperoodon*), which hunts for cuttlefish in the depths of the ocean, has an eye with a more pronounced corneal curvature, which permits more light to reach the peripheral parts of the retina, and there is a corresponding thickening of the rim and its abutment, the sclera. A large cornea is disadvantageous to the whale for architectural and thermal reasons. The toothed whales have larger corneas than the whalebone whales, but this enlargement has been compensated by the thickening of the cornea itself.

Fossil casts or impressions of soft parts like the eyes are of very rare occurrence, so that for evidence in regard to the visual powers of the extinct Eocene zeuglodonts one must examine natural and artificial casts of the cranial cavities of their skulls. These endocranial casts furnish data on the proportions of the several parts of the brain and the relations of the nerves, and also afford much information about the sensory capacities of the animals in question. A number of these brain casts have been described by Fraas, Stromer, Elliot Smith, Andrews, and Dart. The most complete endocranial cast known to us at present was figured and described by Stromer in 1908.

Brains of late Eocene zeuglodonts appear shrivelled and shrunken in comparison with the earlier forms, and there is reason to believe that these animals had not such keen sight as some of their contemporary land dwelling allies. A relative loss of the faculty of sight appears to be indicated by the smallness of the cerebrum and its lack of growth in later forms. The side to side contraction of the area between the olfactory peduncles and the *tuber cinereum* demonstrates the relative atrophy of the optic chiasma in the zeuglodont brain. A reduction of the faculty of sight and possibly of smell involves a compensatory dependence by the zeuglodonts upon the sense of touch in the muzzle. This interpretation, according to Dart (1923), is suggested by the trigeminal specialization in the brains of zeuglodonts. One might infer from the known braincasts that these zeuglodonts experienced some difficulty in adjusting their eyes for under-water vision and that a defective eyesight may have been one of the causes that contributed to the final extinction of this widely distributed group.

In its general features, the cast of the brain of *Prosqualodon* (Dart, 1923) shows a remarkable resemblance to the zeuglodont type, particularly in the cerebellar enlargement and hypertrophy of the trigeminus. On the other hand the brain of *Prosqualodon* has a well defined

optic chiasma, and this area is expanded in contrast to the contracted zeuglodont brain. The widening of this area is correlated with elaborate visual capacities. The brain casts of other extinct Miocene porpoises show that the optic chiasmic region was well developed, and there is nothing to indicate that they differed to any marked degree from their living relatives so far as their visual powers are concerned.

As regards hydrostatic adjustments the whale eye has been adapted to withstand varying pressures as well as the impact of the water when speeding at the surface. It is a well known fact that a vault designed to withstand heavy pressures has to be built so that the directions of the stresses, strains, and pressure forces fall within the abutment. Pütter (1902) points out that the abutment in the whale eye is the enormously thickened sclera. Fluctuations in hydrostatic pressure result in corresponding changes in intraocular pressure. External pressure increases by one atmosphere for each five fathoms of depth. A blue whale (*Sibbaldus musculus*) carried a line straight down for 220 fathoms, where it would have to withstand a pressure of 45 atmospheres or 630 pounds per square inch, and it remained below the surface for 32 minutes. The bottlenosed beaked whale (*Hyperoodon*) and the sperm whale (*Physeter*) are said to descend half a mile and possibly a mile. Pressures at such depths are enormous. At half a mile the pressure is approximately 1178 pounds per square inch and at a depth of a mile about 2349 pounds per square inch.

The chemical adjustments of the whale eye are equally interesting. Constant chemical irritation resulting from contact with sea water necessitates certain adjustments to protect the eye from inflammation or even more serious injury. The tear gland does not secrete a watery liquid, for the eye is no longer in danger of drying up, but instead exudes a greasy substance to protect the cornea from the various chemical substances found in sea water. No trace of the sebaceous Meibomian glands has been found in the eyelids of whales. Furthermore in a number of whales the conjunctiva or mucous outside coating of the eye has been replaced by cornified epithelium. Since the whale eye is subjected to almost constant immersion in sea water of 3 to 4 per cent salt content it does not appear unreasonable to assume that these details represent an adjustment to chemical irritants.

Inasmuch as the cornea of the eye is in direct contact with the water, one might expect that the eye would be protected in some way against continuous cooling below normal body temperature, and curiously enough the freezing point of the liquid media in the whale eye (Sudzuki, 1924) is somewhat lower (Δ 0.66° to 0.72°) than in land mammals. The eye also seems to be sufficiently protected against variations in temperature by the natural replacement of the liquid in the anterior chamber, for inflow and drainage are equal, and the aqueous humor should be maintained at approximately the same temperature as the blood.

OLFACTORY SENSE

Chemical senses, like those of smell and taste, which are closely associated physiologically, require organs that differ considerably in structure and relations. The sense of smell plays an important part in the welfare of many mammals, but cetaceans apparently found less and less need for olfactory structures.

Stromer in 1908 described and figured an unusually complete endocranial cast (fig. 21) *in situ* in a zeuglodont skull from the Qasr-el-Sagha beds of the Fayum,

Egypt. Not merely the cast of the brain but also those of the cavities and sinuses in the region of the narial passages are exposed to view. It is obvious that the sense of smell was still of considerable importance to this zeuglodont, as is shown by the development and peculiar elongation of the olfactory peduncles, which are attached to the ventral surfaces of the cerebral hemispheres in the characteristic mammalian fashion. The rather smooth cerebral hemisphere, which is primarily an olfactory receptive mechanism, is quite different from the convoluted cerebrum of living odontocetes and mysticetes. Only one investigator has had the opportunity to study a series of endocranial casts of Middle and Upper Eocene zeuglodonts. On the basis of these casts, Dart (1923) has concluded that the brains of late Eocene zeuglodonts show that the loss of the sense of smell was gradual and that this loss was accompanied by an excessive development of the trigeminal apparatus, which in a pelagic mammal provides much more information concerning food and enemies.

The whalebone whales (Mysticeti) have olfactory structures, but the retention of the sense of smell may be due in a larger measure to the actual mechanical construction of the skull (see page 44, fig. 2) than to the need of such organs, for the olfactory structures seem to be adapted, as in terrestrial mammals, for smelling through the medium of air. Water never comes in contact with the sinuses in which the olfactory nerves are distributed, and no odors other than those conveyed by water could be recognized when the whales are feeding below the surface. We are therefore at a loss to conceive how cetaceans may smell through the medium of water, inasmuch as the olfactory nerves are distributed in a rather simple manner to the mucous membranes of the olfactory pouches, which hang downward from the dorsal walls of the narial passages. Each of these olfactory diverticula has a slit-like orifice.

The archaic toothed whales of the Upper Eocene have passages for olfactory

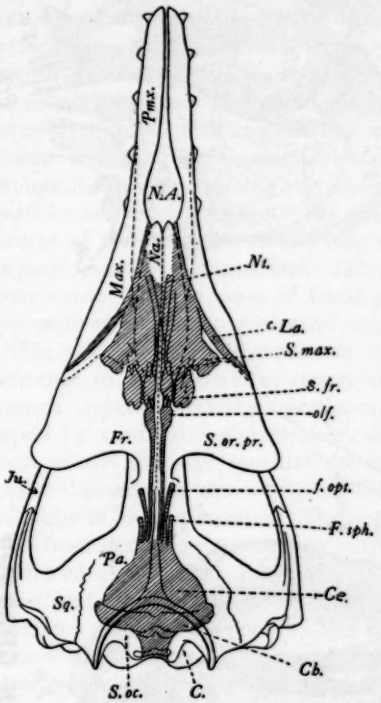
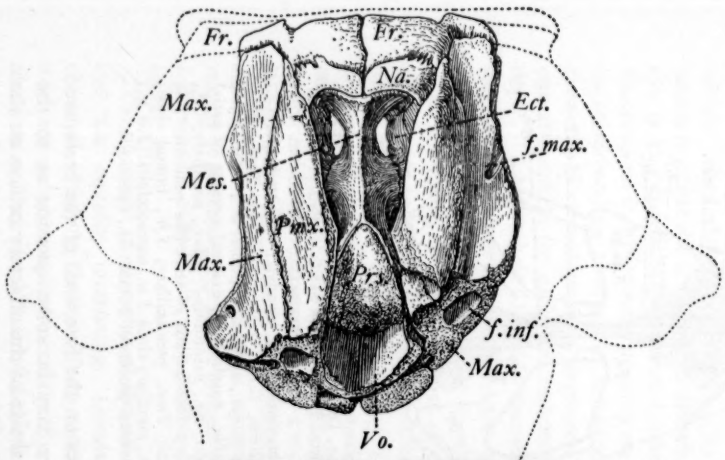


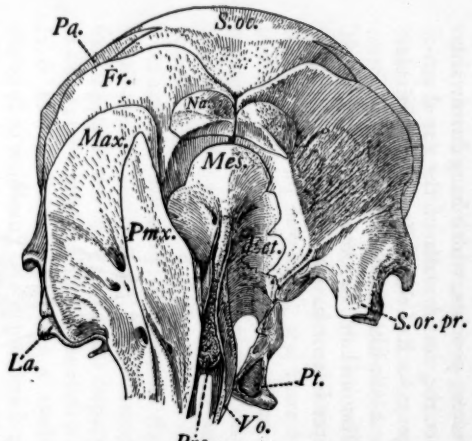
FIG. 21. DIAGRAM ILLUSTRATING POSITION OF ENDOCRANIAL STRUCTURES IN SKULL OF PROZEUGLODON STROMERI

Abbreviations: *C.*, condyle; *Ce.*, cerebrum; *Cb.*, cerebellum; *C.La.*, lachrymal canal; *f.opt.*, optic nerve; *F. sph.*, sphenoidal fissure; *Fr.*, frontal; *Ju.*, jugal; *Na.*, nasal; *N.A.*, external opening of narial passages; *Nt.*, nasoturbinal; *Max.*, maxillary; *Olf.*, olfactory lobe at end of stalk-like peduncle; *Pa.*, parietal; *Pmx.*, premaxillary; *S.fr.*, frontal sinus; *S.max.*, maxillary sinus; *S.oc.*, supraoccipital; *S.or.pr.*, supraorbital process of frontal; *Sq.*, squamosal.

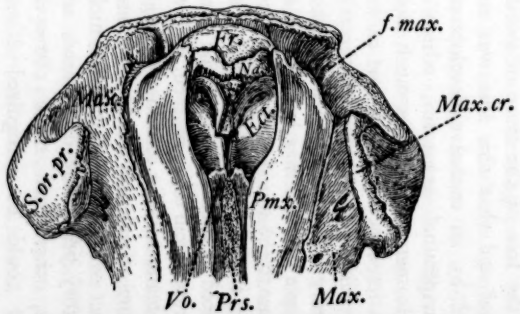
nerves on the fore wall of the braincase. There may be some question as to the actual size of the olfactory orifices on the skull of *Xenorophus sloanii*, for the ethmoid



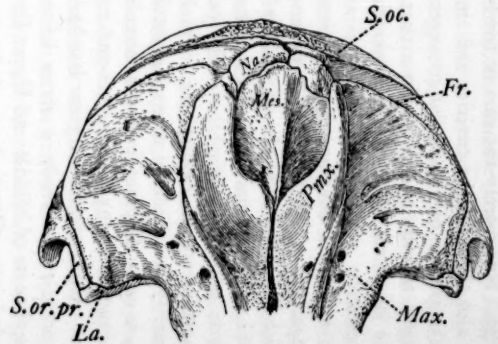
SQUALODON CRASSUS



YG. TURSIOPS TRUNCATUS



ZARHACHIS FLAGELLATOR



AD. TURSIOPS TRUNCATUS

FIG. 33. FRONTAL VIEWS OF SKULLS ILLUSTRATING POSITION OF ETHMOID BONES IN SQUALODON CRASSUS, ZARHACHIS FLAGELLATOR, YOUNG TURSIOPS

bones are missing, but the fontanelle is quite large and the anterior wall of the braincase is unusually thick. The skull of *Archaeodelphis patrius* on the other hand has distinct nasal cavities in front of olfactory foramina of moderate size, which are set off from the forward sloping narial passages. The few endocranial casts of extinct odontocetes that have been described show that at the beginning of the Miocene the olfactory organs had dwindled to very small proportions as compared to *Prozeuglodon*. In the case of *Cyrtodelphis sulcatus* (Dal Piaz, 1905) and *Prosqualodon davidi* (Dart, 1923), the olfactory lobes are attached in a nipple-like fashion to the cerebral hemispheres and the insertion is somewhat higher than in "*Zeuglodon*." All of the squalodonts now known retained remnants of olfactory structures, if our interpretations of the foramina on the fore wall of the braincase are correct. Other extinct Miocene porpoises, including the primitive ziphioid types *Diochotichus* and *Squalodelphis*, have a pair of foramina on the anterior wall of the braincase for the passage of sensory nerves.

The living toothed whales have lost their olfactory organs, though such structures have been found in foetuses. Changes in the relations of the bones in the region where the olfactory nerves originally found passage have resulted in the closure of the opening in the cribriform plate and the concomitant lateral expansion of its component parts, the mesethmoid and ectethmoids, to completely cover the fontanelle on the anterior wall of the braincase between the medial margins of the frontal bones. Mechanical changes in the relations of the component parts of the odontocete type of skull appear to have restricted at first and finally prevented the physiological functioning of the olfactory apparatus. These changes have hastened the final reduction of the dwindling olfactory apparatus of the toothed whales. On the basis of skulls of Miocene porpoises, one would be led to conclude that the passages for the olfactory nerves were reduced by the upward and lateral expansion of the ectethmoids. In many of the late Miocene porpoises and in practically all of the living types, the mesethmoid and ectethmoids have fused to form a continuous sheet of bone, which overspreads the area between the nasal bones and the lateral margins of the trough-like vomer, forming the posterior wall for each narial passage. The general course of the reduction of the olfactory organs can be demonstrated also by comparison of brain casts of fossil porpoises from successive geological stages.

The position of the mesethmoid with reference to the frontals in certain well known types of extinct porpoises is especially instructive and furnishes data from which one may visualize the steps that culminated in the conditions found in skulls of living porpoises. The transition from one stage to another can not be traced at present in a single phyletic series, and recourse must be had to several unrelated types of porpoises. The brief review that follows is necessarily incomplete, but it seems likely that the changes in the relations of the mesethmoid and ectethmoids under discussion clearly indicate the successive stages in the closure of the foramina for the olfactory nerves.

In *Squalodon* the mesethmoid forms the most dorsal portion of the partition between the narial passages, divides the fontanelle between the frontals on the fore wall of the braincase into two large foramina through which the olfactory nerves pass and, extending upward, underlies the nasal bones and provides additional support for the vertex of the skull. The ectethmoids form the external surfaces

of the foramina for the olfactory nerves and overspread the internal borders of the more or less vertical surfaces of the frontals.

In the skull of *Zarhachis flagellator*, the mesethmoid likewise provides some support for the vertex of the skull, but each ectethmoid has grown around the passage for the olfactory nerve and has overspread the lateral surface of the mesethmoid, forming a crescentic foramen. The curved rostral edge of each ectethmoid is the original external edge, and at the caudal end of the foramen is the original internal edge. Succeeding stages in the telescoping of the odontocete skull brought about a further compression of the fore wall of the braincase, causing the mesethmoid to lose its original function of supporting the vertex, and ultimately it came to overspread the frontals below the nasal bones on the posterior wall of the narial passages. In skulls of living porpoises the plate-like bone that sheathes the anterior surfaces of the internal borders of the frontals, conceals the frontal fontanelle, and extends upward to overspread the lower borders of the nasal bones, unquestionably represents the combined mesethmoid and ectethmoids, and corresponds to the cribriform plate of other mammals. In most mammals, the ethmoid plate ossifies into a median mesethmoid bone bounded below on either side by the ectethmoids. These ethmoid bones comprise the cribriform plate, and in the early stages when the mesethmoid and ectethmoids are distinct the olfactory nerves pass out between them.

In a skull of a young *Tursiops truncatus*, the porous plug-like presphenoid rests in the trough of the vomer and the thin lateral walls of the latter embrace the lower half of this bone. Dorsally there is a second thin curved bone, coextensive with the internal and posterior walls of the narial passage, which fits into a groove on the upper margin of the thin lateral wall of the vomer and in addition sheathes the inner borders of the frontals outside the frontal fontanelle. One of these bones is present in each narial passage. These bones fulfill the requirements of the ectethmoids. The inner margins of the lateral plate-like ectethmoids do not meet the mesethmoid above the presphenoid as in an older individual. The mesethmoid no longer supports the vertex of the cranium and has been crowded out of its original position to overspread the anterior wall of the braincase below the nasal bones. Inferiorly on each side it has fused with the corresponding ectethmoid. On the internal margin of each ectethmoid is an incomplete fissure or vestigial foramen, which marks the original position of the orifice for the olfactory nerve. In older individuals these ethmoid bones completely fuse and form a continuous sheet of bone, which extends upward toward the vertex, overspreading the lower borders of the nasal bones. The olfactory nerves were thus effectively shut off from the narial passages by the development of this bony plate.

ACOUSTIC SENSE

Life in the water necessitated a remodeling of the organ of hearing so that it would function under the changed conditions. The initial stages in the transformation of an organ of hearing designed for the perception of air-borne sounds to one adapted to receive water-borne sounds are unknown, for the earliest known zeuglodonts have the osseous portions of this organ as highly developed as any of the living whales. The ancestors of the living cetaceans must have had functional ear drums just as have man and other mammals, but in the course of geological

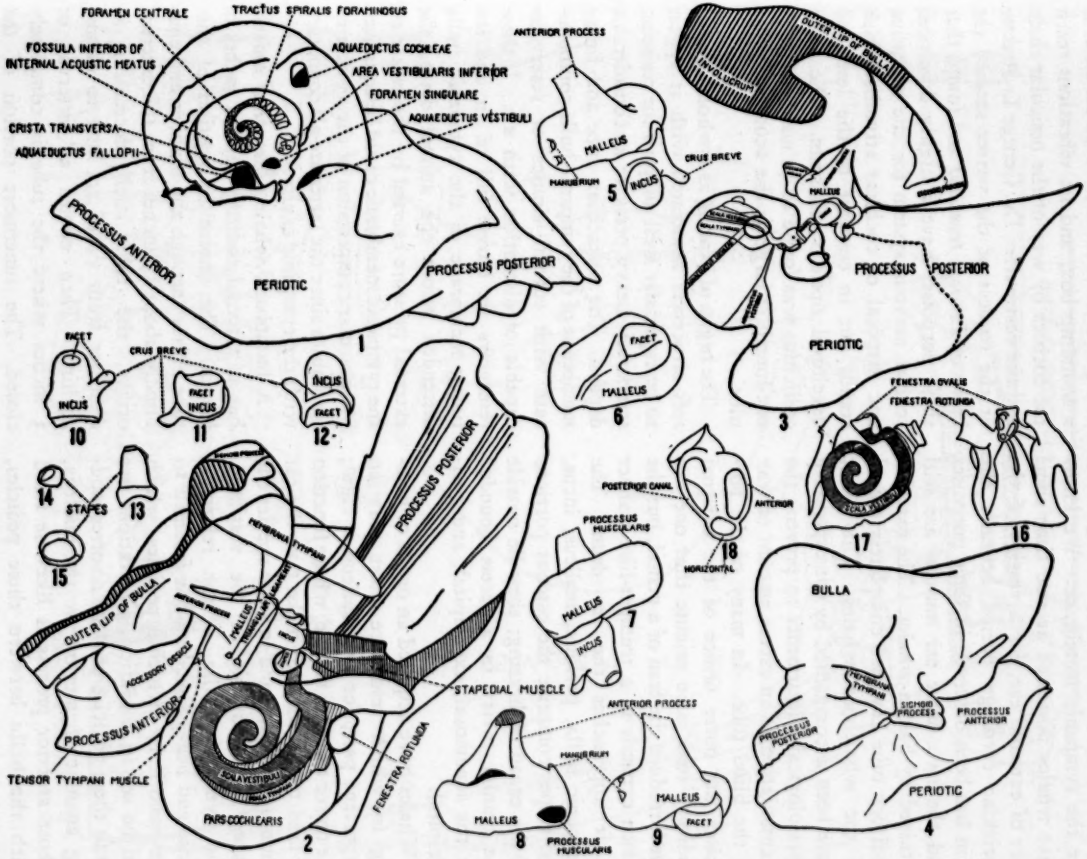


FIG. 23. DIAGRAMS ILLUSTRATING AUDITORY APPARATUS OF MONODON MONOCEROS

time the osseous portions of the inner ear have undergone certain changes, which brought about a diminishing utility for the tympanic membrane. We know that whales possessed at one time some sort of external ear, for a vestige of the auricular cartilage buried beneath the skin has been observed in some porpoises and the two outer ear muscles are still retained by baleen whales. The external auditory tube has been completely closed in the whalebone whales. This must have been accompanied by corresponding physiological adjustments to prevent the accumulation of an excess amount of wax in the blind tube. In many of the porpoises the outer orifice of the external auditory tube is so minute that one can not introduce the lead of a pencil, but the lumen expands in a trumpet-like manner as it approaches the ear drum. The tympanic bulla, periotic, malleus, incus, and stapes comprise the osseous portions of the organ of hearing; they lie outside the cranial cavity in a recess bounded by the squamosal, exoccipital, and basioccipital.

Whales have acquired an organ of hearing in which resonance must play an important part, for the malleus is rigid; the tensor tympani muscle, whose function in land mammals is to make taut the ear drum, is vestigial; and in some species the stapes is immovable in the vestibule. The tympanic bulla is the relatively dense and heavy sounding box fastened to the periotic by two thin pedicles, which can be set in vibration. Vibrations set up in these pedicles produce a corresponding amount of motion in the malleus, whose anterior process is likewise fused with the bulla between these pedicles, and it in turn transmits these vibrations to the incus and stapes. Another mechanical arrangement is thus acquired to take over the function ordinarily performed by the ear drum. Water-borne sound vibrations transmitted to the air contained in the tympanic bulla cause it to function as a sounding box, and its vibrations reach the cochlea by way of the ossicular chain and the vestibule. Dr. George L. Streeter at the request of the writer studied the brain of *Tursiops truncatus* and found that these porpoises have a highly developed central nervous system for the reception and disposal of cochlear stimuli, which stands out in contrast to the less well developed optic mechanism. The optic colliculus was found to be not more than one-fourth as large as the acoustic colliculus.

The organ of hearing as a whole and the soft structures associated with it appear to be especially well adapted for resisting temporary heavy pressure at considerable depths. The eustachian tube and lining membrane of the tympanic bulla communicate with several sinuses or reservoirs capable of distention with air. If these reservoirs are blown full of air and the lining membrane of the tympanic bulla distended before the animal dives, the external pressure exerted by the water on the tympanic membrane could be equalized by muscular compression of the associated air sinuses since the latter are all connected with the tympanic cavity.

A humpback whale (*Megaptera nodosa*) has an external auditory tube 21 inches in length. The outermost portion of this tube passes through the blubber and ends blindly about $5\frac{1}{2}$ inches from the external orifice, the tube itself decreasing in diameter from $\frac{1}{10}$ of an inch to almost nothing. Then comes an interval of 3 inches where the tube is completely closed. The innermost portion of the tube widens to a diameter of more than an inch and the walls are invariably collapsed. The tympanic membrane is in many respects the most remarkable structure

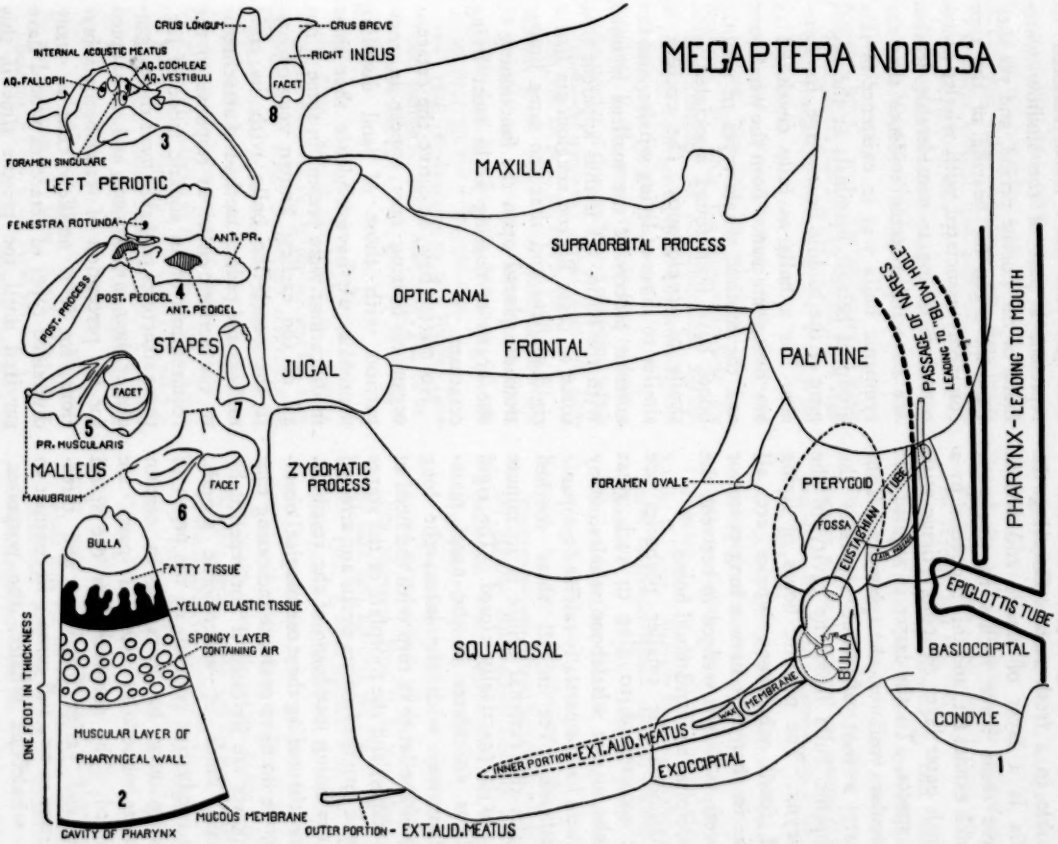


FIG. 24. DIAGRAMS ILLUSTRATING AUDITORY APPARATUS OF MEGAPTERA NODOSA

connected with the organ of hearing. It is a finger-shaped structure, measuring about 3½ inches in length, and is soft and flexible in a fresh state. Covering the bulla is a layer of elastic and fibrous tissue some three inches in thickness, which exudes fat, and this is covered by a 4 inch outer layer of spongy tissue with air spaces. To the latter is applied the muscular wall of the pharynx. Thus nearly a foot of tissue separates the tympanic bulla from the cavity of the pharynx. The periotic bones of living and fossil whalebone whales are all alike in that they have a long posterior process, which is wedged in between the exoccipital and squamosal bones.

Although the smaller porpoises are not accustomed to dive to such great depths as the whalebone whales, many of them have a partially calcified tympanic membrane. Yet in all these toothed whales the external orifice is so minute that it is practically closed. The rigid malleus articulates in the usual mammalian way with the incus, the long crus of the latter in turn with the head of the stapes, and the footplate of the stapes is sunk into the fenestra ovalis and arrested by the lining membrane of the vestibule. Notwithstanding these osteological obstacles, we do have evidence indicating that porpoises are irritated if not repelled by certain kinds of water-borne sounds. The conductive portions of the organ of hearing may be defective in certain respects, but the essential parts are retained. The cochlea is of the spiral type and varies from one and three-quarters to two full turns. In contrast to the whalebone whales, the porpoises, dolphins, sperm whales, beaked whales, and their relatives all have the ear bones attached to the skull by ligaments.

Zeuglodonts have been assumed to represent a part of the shallow water fauna of the Eocene period, and yet they have an organ for hearing of the type commonly associated with whales accustomed to diving to considerable depths. We have indisputable evidence that the tympanic bulla was in existence in this group of pelagic mammals at the beginning of the Middle Eocene age, for *Protocetus* has a bulla as fully developed as any living cetacean. Both the whalebone and the toothed whale types of periotic bones have been found associated with skulls of zeuglodonts. The cochlea is similar to those of living whales, and the anterior process of the malleus is fused with the bulla. It is thus apparent that some of these Eocene zeuglodonts had a rigid malleus and that the same limitations are placed upon the functioning of the organ of nearing as in most living cetaceans.

No matter how defective the cetacean organ of hearing may appear in comparison with those of land dwelling mammals, we have evidence that these modifications were present in some if not all of the earliest known zeuglodonts. If the conch-like bulla with its rigid malleus and pedicle method of attachment to the periotic arose in response to the requirements of an aquatic mode of life, these structures probably meet the exigencies of their environment, and are adapted for the perception of water-borne vibrations, for it is unlikely that so many diversified types of cetaceans would have survived until the present time if this organ were unsuited for their purposes.

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THE EFFECT OF CARBON DIOXIDE ON BACTERIA

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IN 1848 Bethell patented a process for preserving milk by carbonation, which consisted in first boiling the milk to expel all the air contained in it and then saturating it with carbon dioxide. The milk, it was claimed, remained fresh for a long time after being exposed to the air. This process is more or less of prehistoric interest, since no evidence has survived to show how successful it was in its application.

DESTRUCTIVE EFFECTS OF CARBON DIOXIDE

Pasteur and Joubert (1877) observed that *B. anthracis* is killed in carbon dioxide. No mention is made of the media that were used in their experiment, nor is it stated how long the exposure to the gas continued, or how much carbon dioxide was required to react fatally to *B. anthracis*. Szpilman (1880) suggests that the above claim should be qualified somewhat, since he, Szpilman, showed definitely that from five to eight hours' exposure to an almost pure atmosphere of carbon dioxide did not kill *B. anthracis*, or even alter the pathogenicity. Grossmann and Mayerhausen report (1881) that CO_2 does not kill bacteria, but that it inhibits motility. Small amounts of CO_2 increased motility. Buchner (1885) has shown that the effect of carbon dioxide gas is variable. It inhibited Koch's Vibrio, but development was obtained with Fitch's Aethylbacillus, the Napel cholera bacillus and *Bact. typhosum*.

In 1885 and 1886 a series of papers by Pfuhl, Sohnke, Schaffer and Freudenreich, and Kolbe appeared. The investigations of Pfuhl and Sohnke dealt with the microörganisms found in carbonated waters. Schaffer and Freudenreich reported that typhoid and anthrax bacilli were unaffected in broth cultures under seven atmospheres of carbon dioxide pressure. Kolbe's work was an attempt to preserve meat and fruit in an atmosphere of carbon dioxide. Beef could be preserved for eighteen days, while mutton showed spoilage in a very short time.

Liborius (1886) failed in his attempts to initiate growth of *Cl. foetidum*, *Cl. polypiformis*, *Cl. oedematis-maligni* and *B. pseudo-oedematis* when carbon dioxide was passed through the medium. However, when it was passed over the surface of the medium some growth was obtained. Bolton (1886) reported a limited number of experiments with *M. aquatilis* and *B. erythosporus*. The results were erratic; inhibition was obtained in some cases but not in others. The duration of CO_2 treatment is not given. These experiments were carried out in water containing only traces of organic matter. Destruction of bacteria was also evident under hydrogen.

Leone's work appeared in a German translation in 1886, and concerned itself with the reduction of bacterial numbers in the city water of Munich. Reduction was obtained, but complete sterilization was never reported. The statement was made that pressure was not a factor in

these experiments, since carbon dioxide was applied at atmospheric pressure. The experiments as a whole offer only a very limited amount of data.

BACTERIA IN CARBONATED WATERS

Hochstetter's work (1887) was on the behavior of microörganisms in artificial carbonated waters, city water of Berlin and distilled water. This work has remained as a source of valuable information, and has probably not been surpassed in extent and comprehensiveness. The experiments included pure culture studies of *M. aurantiaca*, *E. prodigiosus*, pink yeast, a green fluorescent bacillus, a yellow bacillus, *M. tetragenus*, *Bact. lepisepticum*, *B. anthracis* (vegetative cells and spores), *Bact. typhosum*, alpha-bacillus, *V. cholerae*, spores of *Aspergillus flavescens*, and Finkler-Prior's bacillus. These organisms fell into three groups, according to their tolerance for carbon dioxide: (1) those which were viable for only a short time, (2) those which remained viable for a few weeks, and (3) those which survived for many weeks and even months.

According to Hochstetter's observations, there is no danger from cholera through carbonated waters, but the danger from typhoid fever is not altogether removed, since *Bact. typhosum* remains viable for from five to seven days. Epidemics of typhoid traced to carbonated waters occurred in Mainz in 1884. The author was able to control the development of bacteria in experimentally carbonated waters. Numerous organisms were found, however, in bottled beverages prepared under factory conditions.

Sirotinin (1888) reported a limited number of trials with *V. cholerae*, the Finkler-Prior spirillum, *Staph. albus*, *B. anthracis*, *B. cuniculicida* and *Bact. murisepticum*. There was complete inhibition of the last two organisms.

Fränkel (1889) reported a comprehensive series of experiments comprising forty different bacterial species. Gelatin medium was used in Esmarch tubes, and carbon dioxide gas was applied while the medium was still soft. It is noteworthy that inhibition or even killing was obtained with the organisms which are very sensitive to acid, for example *V. cholerae*. His observations were briefly summarized as follows: Certain common types of bacteria were able to develop in carbon dioxide as well as in the ordinary atmosphere; others were retarded, and a third group would not grow at room temperature, but would develop in CO_2 at higher incubation temperature. The effect of carbon dioxide was also tried on the saprophytic bacteria. The influence was not wholly inhibitive. The author believed that his results may be taken as a proof that carbon dioxide is a preservative or germicide. He stated at the same time that, in spite of this growth-inhibiting, or at times even killing, action, carbon dioxide should not be regarded as a sure means of preventing decomposition.

Weakening of pathogenic bacteria by CO_2 does not occur, according to him. The author also pointed out that in view of the unhindered growth of *Bact. typhosum* in a stream of CO_2, the so-called "harmlessness" of carbonated waters must be liberally interpreted.

Fränkel's work is similar to Hochstetter's in comprehensiveness, and, although conducted in a somewhat different manner, the conclusions arrived at are identical. Fränkel also observed that the reaction of the gelatin medium changed under the stream of carbon dioxide. He believed, however, that this change in reaction was inconsequen-

tial. It is, nevertheless, interesting to note that the acid-sensitive microorganisms, such as *V. cholerae*, *B. anthracis*, etc., were most easily inhibited.

Frankland (1889) reported his experiments with *V. cholerae*, the Finkler-Prior vibrio and the organism of blue-green pus. His results are on the whole in accord with Fränkel's findings. He pointed out that certain differences in their results may be explained by variability in resistance of strains used. He confirmed Fränkel's observation that the majority of the organisms succumb readily. However, a small per cent remained alive and even multiplied to a certain extent.

Scala and Sanfelice (1891) investigated the effect of dissolved carbon dioxide in natural waters. It appeared that the pathogenic organisms, *V. cholerae*, *B. anthracis*, *Staph. aureus* and *albus*, *Bact. typhosum* and *Bact. lepisepticum* were not affected by the quantities of CO_2 naturally dissolved in water at 15°C. When the water was saturated with CO_2, *V. cholerae* and *B. anthracis* were injured, while others remained apparently indifferent. Carbon dioxide under pressure in soda-water was injurious to *B. subtilis*, while *Proteus vulgaris* remained unaffected. Spores of *B. subtilis* and *B. anthracis* did not germinate.

BACTERIA REQUIRING CARBON DIOXIDE

During the years 1890 to 1899 a very interesting observation was made and proven to be a fact, namely that though carbon dioxide exerts injurious effects on certain bacterial species, it is actually required by others. Vinogradsky (1890) and Vinogradsky and Omeliansky (1899) in a series of articles showed that the nitrifying organisms require carbon dioxide, utilizing it as a source of carbon. Godlewsky (1892) confirmed the original observation of Vinogradsky. These findings have been confirmed more recently by Meyerhof (1916–17) and Bonazzi (1921).

Considerable controversy developed between d'Arsonval and Charrin (1893) and Sabrazès and Bazin (1893). The former had recommended for the sterilization of organic filtrates an application of carbon dioxide under pressure of 50 to 60 atmospheres. They also reported, however, that *Ps. pyocyanea* cultures in broth were not killed under the given pressure of carbon dioxide during six hours' exposure. Sabrazès and Bazin repeated the work of d'Arsonval, but could not confirm his claims, even at higher pressures than those indicated by d'Arsonval, who suggested that certain organic liquids, such as blood, milk and urine, could be preserved in this manner. Sabrazès and Bazin experimented with *Staph. aureus*, *Bact. coli*, *B. anthracis* and *Bact. typhosum*, arriving at the conclusion that pressures of 90 atmospheres and beyond do not injure *B. anthracis* or *Staph. aureus*.

It would be of doubtful value to employ CO_2 for sterilization of organic liquids within the time limits fixed by d'Arsonval. In his reply to Sabrazès' criticism, d'Arsonval claimed that the differences in results were obviously due to differences in experimental technic. The sterilization in his experiments was effected with filtrates made up with glycerine to 15 or 20° Baumé. It was, therefore, the combined action of glycerin and of CO_2 under pressure which was responsible. He states very judiciously that "quant aux conditions de pression, de durée, de température, de composition chimique et de milieu nécessaires pour tuer les différents microbes pathogènes, c'est là une détermination pour laquelle je ne me suis pas senti une compétence suffisante."

Slater (1893) published a report on his examination of artificial carbonated waters sold and prepared under factory conditions. This was supplemented by some observations on water supplies used in their preparation and on experimentally prepared and inoculated carbonated waters. Slater used *Ps. fluorescens* liq., *Bact. coli-communis*, *Staph. aureus*, *Bact. typhosum*, *V. cholerae* and the Finkler-Prior spirillum. His experiments showed that, while killing or inhibition could be effected, it varied with the organism in question. The destructive action was intensified in storage, being most noticeable after three weeks, but not necessarily of a constant occurrence. He observed that artificial carbonated waters are by no means sterile, although the numbers of bacteria present are not an index of the original purity of water used in the preparation.

Haenle's work (1905) supplements that of Slater. He made further observations on the necessity of cleanliness and sanitary conditions of bottling plants. Natural mineral waters are normally almost sterile or completely sterile when issuing from the ground. Differences were observed with different kinds of bottles, i.e., siphons, corked, or capped bottles. The siphons were apparently the most sanitary. When a sample contained more than 300 organisms per cubic centimeter it was considered by him as having been stored in dirty bottles.

A series of articles which appeared in 1895 to 1899 by Czaplewsky, Draer, and Morgenroth could not be obtained in the original. It appears, however, from available abstracts that these reports were in perfect accord with those mentioned here, and in general emphasize the necessity of more or less prolonged storage of carbonated waters intended for human consumption.

STIMULATING ACTION ON PIGMENTATION

Lubinski (1894) and Neumann (1897) observed that pigment-producing organisms such as *Staph. aureus* are devoid of color under anaerobic conditions, but develop abundant pigmentation when reëxposed to air. The cultures which were grown in carbon dioxide and had lost their color had the pigmentation restored much more rapidly than those which were subjected to hydrogen. Consequently, the conclusion is drawn that carbon dioxide exercises a certain stimulating action on pigmentation.

The present writer's experience has shown that this observation holds true also with *E. prodigiosus*. In an atmosphere enriched with 1 per cent carbon dioxide very intense pigmentation bordering on a dark maroon was obtained. By reducing the carbon dioxide content below that which is normally found in the air only a very slight color was obtained, that is, a faint shade of pink.

Hoffmann's work (1906) comprised a series of experiments with carbon dioxide on the colon-typhoid group in water, nutrient broth and milk. High pressures of carbon dioxide were used. This author realized that a very small number of bacteria may persist in the medium after the treatment with CO_2; hence he used an enrichment cultivation method. By adding 1 per cent peptone broth to the liquid after the carbonation, and incubating the whole quantity, he was able to obtain subsequent growth on plates and in broth, whereas he failed to detect viable organisms by the usual inoculation transfer method. Sterilization in water suspension was obtained at 50 atmospheres of carbon dioxide in from 2 to 3 hours with *Bact. coli* and the dysentery bacillus. Minute traces of organic matter or other nutrient material when present tended to render the results irregular.

EFFECT ON BACTERIA IN MILK

Hoffmann's experiments with milk were unique. No other work of a similar nature has come under the writer's observation. This author investigated the effect of carbon dioxide on the bacteria in milk, and on the milk itself. Under 50 atmospheres of carbon dioxide the bacterial count could be materially reduced in 48 hours, (from 1,012,930 at the start to 7,276); but complete sterilization was evidently never obtained. The results were no better when the milk was heated to 50°C for 20 minutes. The reduction was more marked, but a slow curdling of milk took place. The observation was made that carbon dioxide exerts considerable influence on sterile milk. After allowing 50 atmospheres of carbon dioxide to act at 56° for 24 hours on raw milk, the casein could easily be separated from the whey. It was observed that samples of raw milk under 10 atmospheres of carbon dioxide pressure remained in apparently good condition for at least 72 hours. The untreated samples curdled in 24 hours. The author concluded that the question of milk sterilization by CO_2 was far from satisfactory.

Altana (1907) experimented with 75 different organisms, including higher bacteria, moulds and yeasts, and according to his results divided the organisms studied into three different groups as follows: (a) those which were completely inhibited by carbon dioxide (high tension), (2) those that were not affected at all by this agent, and (3) an intermediate group composed of species that were more or less variable.

Van Slyke and Bosworth (1907) investigated the preserving action of CO_2 on milk. Lactic fermentation was delayed in CO_2 under pressure. No noticeable effect was observed under ordinary atmospheric pressure, however.

Berghaus (1907) subjected thirteen species of microörganisms to various pressures, under carbon dioxide. His list comprised the following: *V. cholerae*, *B. anthracis*, *Bact. typhosum*, *Bact. coli*, *Bact. fecalis-alkaligenes*, *Bact. enteritidis* Gaertner, *Bact. dysenteriae* (Shiga-Kruse and Flexner), *Bact. paratyphosum* A and B, *Staph. aureus*, *Ps. pyocyanea* and *Proteus vulgaris*. These organisms were subjected to carbon dioxide on freshly poured agar plates for a period of 24 hours, at 37°C. The strains under investigation were divided into three groups as follows: (1) *V. cholerae* (killed in 24 hours at one atmosphere pressure), (2) *B. anthracis* and *Bact. fecalis-alkaligenes* (growth inhibited in 24 hours, but no killing), and (3) *Bact. coli* and *Bact. enteritidis* (able to develop under two atmospheres of carbon dioxide pressure). Variations in resistance were shown by various strains of *Bact. coli*. Four of the strains required 15 atmospheres of carbon dioxide, while with two other strains a pressure of 9 atmospheres was sufficient to kill.

During the period from 1911 to 1915 a series of articles by the following investigators appeared, dealing with various phases of bacteriology in carbonated beverages: Klein (1911), Young and Sherwood (1911), Eldson (1912), Allen, La-Bach, Pinnell and Brown (1915) and Colin (1915). Aside from variations in experimental technic, different organisms studied, and the objects or aims which prompted the investigations, certain observations are common to all of these works. According to them, carbonated beverages found on the market may or may not be free from living microörganisms. Reduction could be obtained with the pathogenic forms, but not complete sterilization. The sources of microörganisms in commercial products are evidently unclean bottles and unsanitary conditions

of the plant. The work of Allen, LaBach, Pinnell and Brown is particularly illuminating.

Colin's (1915) experiments were conducted with sterile water, into which broth cultures of the test organisms were introduced. Pressures varying from 10 to 24 kilos were then applied for varying lengths of time, generally from one to twelve hours. *Bact. typhosum*, *Bact. coli*, *Bact. dysenteriae* (Shiga), *V. cholerae*, *Ps. pyocyanea*, *C. diphtheriae* and *B. subtilis* were subjected to study under carbon dioxide pressures. Sterilization was effected with *Bact. typhosum* in 20 hours or more at 10 kilograms CO_2 pressure. With *C. diphtheriae* sterilization was obtained at 10, 15, and 20 atmospheres after 24, 9, and 3 hours respectively. *Bact. coli* persisted for 5 days under 25 kilo pressure.

In 1911 another departure from the study of the destructive effects of carbon dioxide on bacteria occurred. Lieske reported that *Spirophyllum ferrugineum* is benefited by the presence of carbon dioxide. The growth of the organism was considerably increased by this gas, and inhibited by the presence of organic matter.

Wherry and Oliver (1916), following Nowak's work of 1908, grew the gonococcus and several other organisms under reduced oxygen tension. It was emphasized that some parasitic species could be isolated or made to grow considerably better under partial tension than under full anaerobic or aerobic conditions. No mention is made of carbon dioxide influence. Five bacterial species in all were used, including *Bact. typhosum*.

Cohen and Markle (1916) reported a successful primary isolation of meningococcus under partial oxygen tension, but no mention is made of any possible influence of carbon dioxide as such.

Wherry and Ervin (1918) furnished some experimental data which indicated that carbon dioxide is necessary for the growth of *M. tuberculosis*. Saprophytic and non-saprophytic strains were used in the experiments, and were found to be alike in their failure to grow in the absence of carbon dioxide.

Larsen, Hartzell and Diehl (1918), in an effort to produce antigenic material in a diffused state, resorted to high pressures under various gases. Carbon dioxide was fatal to *Bact. typhosum*, *Bact. coli*, *M. tuberculosis*, *Ps. pyocyanea*, staphylococci, streptococci and pneumococci in from 1.5 to 2.5 hours. Pressures of carbon dioxide under 40 atmospheres did not produce any visible effect on the bacteria studied. The action of this gas under pressure was more destructive in distilled water than in nutrient broth. Yeast cells resisted it much longer than 24 hours.

BENEFICIAL EFFECT OF CARBON DIOXIDE

Cohen and Fleming (1918) made use of the tandem cultivation method in their meningococcus studies; they also supplied carbon dioxide gas as such, in amounts varying from 10 to 75 per cent. Their results showed that as good growth could be obtained by supplying the gaseous CO_2 as with the *B. subtilis* culture method. The optimum concentration varied from 10 to 30 per cent carbon dioxide. With from 50 to 75 per cent of the gas the growth was scant. Their explanation was that the CO_2 dilutes the oxygen and thereby helps the growth; i.e., the partial tension phase was strongly emphasized.

In the same year (1918) MacKenzie reported that 22 per cent carbon dioxide was bactericidal for the meningococcus in Ringer-Locke solution, in 20 minutes. Ruediger (1919) confirmed the partial tension idea by obtaining good growth of the meningococcus in stoppered tubes. There was no growth when the tubes were

left open. It may be presumed that the CO_2 liberated during respiration diluted the oxygen.

Chapin (1918), following Wherry's technique in primary isolation of the gonococcus, carried the method a point further, and applied carbon dioxide gas directly. He obtained good growth over a wide variety of concentrations. The author also suggested that the growth of *B. subtilis* not only diminishes oxygen, but supplies carbon dioxide as well. Hence, the same object could be attained by supplying CO_2 or by placing a lighted candle in the jar with the plates.

Cohen's work was severely criticized by Gates (1919). The latter claimed that ascribing microaerophilic properties to the meningococcus was an error, since the organisms would grow successfully in atmospheres of 24, 32 and 40 per cent oxygen. Reduction of oxygen to 15 and 18 per cent respectively showed no inhibitive or benefitting influence over the control plates kept under ordinary atmospheric conditions. Growths were equally good at any points within 10 and 30 per cent carbon dioxide, as long as the reaction of the medium remained favorable. The author concluded that if there was any effect from carbon dioxide it was due to changing the reaction of the medium and making it favorable for the meningococcus.

St. John (1919) denied that there is any influence exerted by CO_2 on the meningococcus, and attributed the beneficial results entirely to the increased moisture content in the closed system. Kohman (1919) supported the view that carbon dioxide is beneficial to the meningococcus, by delicately adjusting the reaction to the optimum pH range of the meningococcus. By this adjustment a buffer system was created and further deviations of pH prevented.

Stokes (1920), and Gershenfeld (1920) published their results of examinations of carbonated beverages, undertaken largely from the public health standpoint. It appears, according to them, that a very large per cent of carbonated beverages on the market showed high bacterial counts. The possibility of intestinal infection through the consumption of such beverages is pointed out.

The interest in primary cultivation of the gonococcus and other organisms of this type under increased carbon dioxide tention, or sometimes reduced oxygen tension, has not in the least abated. Herrold (1920) described a modification of the partial tension method whereby good results were obtained. This consisted in inverting the plates inoculated with gonorrheal material over a plate inoculated with *B. subtilis*, and joining the two plates with a rubber band. Bicarbonate was used also, instead of *B. subtilis* in the lower plate. By the addition of 1 per cent sulphuric acid carbon dioxide was liberated and the conditions necessary for growth furnished.

Swartz and Davis (1920) created partial tension conditions by heating the tubes and sealing them with rubber stoppers. Upon cooling, reduced tension was obtained. This facilitated the handling of a large number of cultures.

Huddleson (1920) changed from the *B. subtilis* tandem culture method for culturing *Bact. abortus* to one in which an atmosphere containing 10 per cent carbon dioxide by volume was employed. The same object, i.e., increased CO_2 content, was attained by him when the culture tubes were sealed. His observations are in accord with those of Cohen and Fleming (1918), and of Ruediger (1919), with the meningococcus, and of Chapin (1918) with the gonococcus. He apparently recognized the importance of carbon dioxide

as such in the cultivation of *Bact. abortus*, rather than the necessity of reduced oxygen.

ADAPTATION OF BACTERIA TO DIFFERENT GASES

Rockwell and McKann (1921) investigated the effects of various gaseous environments on the growth of the gonococcus. Their results showed that this organism could be trained to tolerate rather high concentrations of hydrogen, carbon dioxide and oxygen, when mixed with air or in combination with each other. When a certain strain had become adapted to grow under high concentration of hydrogen, growth was inhibited by the presence of much oxygen and carbon dioxide. As high as 100 per cent of any one of these gases could be used in growing the organism. They concluded, therefore, that the gonococcus can be made to grow under various gaseous environments. It is believed by them that such expressions as aerobic, anaerobic or partial-tension strains, are expressions of the previous gaseous adaptations in nature.

Rockwell (1921) studied the gaseous requirements of the gonococcus, *B. subtilis*, *M. tuberculosis* 801, 802, and 803, *Bact. coli*, *Staph. aureus*, *Prot. vulgaris*, and *B. anthracis; Cl. welchii* and *Cl. tetani* were the anaerobes used. Enclosing the cultures either in hydrogen or nitrogen, or under anaerobic conditions with pyrogallol, it was observed that the cultures failed to grow. If, however, the respiratory CO_2 was not removed, or if CO_2 was supplied to cultures under nitrogen, growth followed. The author concluded that growth of the aerobic bacteria and those of the facultative group is in some way favored by CO_2.

Torrey and Buckell (1921) refuted the idea of a reduced oxygen requirement for the gonococcus, and believed that success in obtaining growth in a closed system is due entirely to the increased moisture retained in the medium or in the air over the medium.

Corper, Gauss and Reusch (1921) reported inhibition of *M. tuberculosis* without carbon dioxide, and inhibition of growth when the CO_2 approached 3 per cent; they considered 12 per cent CO_2 definitely tuberculocidal. In further studies concerning the importance of the growth of tubercle bacilli as determined by gaseous tension Corper, Lurie and Uyei (1927) conclude that a slightly better growth is observed in an atmosphere enriched with carbon dioxide than without the added CO_2.

COLON-TYPHOID BACTERIA IN CARBONATED WATERS

Koser and Skinner (1922) investigated the viability of the colon-typhoid group of organisms in carbonated waters and carbonated beverages. In their experiments the waters and beverages under observation were prepared under experimental conditions simulating those of the factory as far as possible. The authors came to the conclusion that the chief bactericidal influence of CO_2 was due to the increased hydrogen ion concentration in the solution. *Bact. coli* showed considerable resistance to carbon dioxide and could be recovered from various non-acid beverages after 7 days under 28 lbs. pressure at 24°C. In acid beverages the longevity of *Bact. coli* was reduced. The plates were sterile in 3 days, but not in 24 hours. When kept at 1°C, viable organisms were not recovered in 10 cc. amounts of the liquids after one month. *Bact. typhosum* was less resistant. It was evidently destroyed in 24 hours at 25 pounds pressure, at room temperature. At 1°C, this organism persisted for 4 days. Paratyphosum B. was positive in 10 cc.

after 48 hours at 23 pounds pressure and 24°C. At 1°C. the same organism was found to be alive in 10 cc. after 10 days. The spores of *B. mesentericus* and *B. subtilis* were found to persist in carbonated water in their original numbers after one month.

Prucha, Brannon and Ambrose (1922) investigated the effect of carbon dioxide on bacteria in milk and ice cream. It was found that there was no destruction of bacteria when the milk containing *Bact. coli* and *Bact. typhosum* was subjected to from 10 to 30 pounds extra pressure, under carbon dioxide. Under 20 pounds pressure there was an increase from 47,000,000 to 153,000,000 per cc. of milk. They also showed that there was no decrease of bacteria in ice cream, due to carbon dioxide. Even after six months in storage the carbonated ice cream had as many bacteria per cc. as the plain ice cream.

Erickson and Albert (1922) reported their experiments with various methods of producing reduced oxygen-tension for the gonococcus, and came to the conclusion that the beneficial effects are entirely due to an increased amount of moisture. Fitch (1922), when using Huddleson's method for enriching the atmosphere with CO_2, found difficulty from liberated chlorine. He grew duplicate sets of cultures, one in carbon dioxide and the other set in hydrogen, and evidently found no difference in favor of carbon dioxide. He concluded that Huddleson's claim for a specific action of CO_2 is not proven, and that this gas probably does nothing more than to dilute the oxygen.

Lorentz (1923) observed that the diphtheria organism, when grown under CO_2, became longer and more slender. The granules were increased in size and thickened. The number of positive diphtheria cases was found to be 30 per cent higher when the field cultures were grown under added CO_2, instead of ordinary air.

Rockwell (1923) reported additional work on gaseous environmental studies, on ten different organisms. The list comprises *B. subtilis*, *M. tuberculosis* (saprophytic strain), *Prot. vulgaris*, *Staph. aureus*, *Cl. welchii*, an anaerobe from hide, pneumococcus pus, streptococcus pus, and the meningococcus. Throughout the experiment, conducted under aerobic conditions, with nitrogen gas, nitrogen and carbon dioxide, and under conditions of anaerobiosis with pyrogallol and partial tension, growth was obtained under nitrogen and carbon dioxide with all of the various organisms used. Further division of partial-tension organisms was made by him according to their tolerance for oxygen.

Donald, Jones and MacLeon (1924) reported experimental work on artificially inoculated beverages. *Bact. coli* and *Bact. typhosum* were used as the test organisms. A study of the curves shows a very interesting relationship between high pressure and storage. The decline in bacterial numbers seems directly proportional to both. With a pressure of 95 pounds the beverages were apparently sterile after 5 days at room temperature. The curve shows that with 15 pounds bottling pressure there was a decline, but after 6 weeks the curve is still above the zero line. At 37.5°C. the bactericidal effect of CO_2 caused sterilization in one week. In general, it is apparent that after 34 days at 20°C., and at 37.5°C., the beverages showed bacteria present under all conditions and pressures of the experiment. The pressures were 70 and 45 pounds respectively. A second series of beverages was prepared and inoculated very lightly. *Bact. typhosum* did not show any rise in numbers under high pressure (70 pounds).

Bact. coli gave an increased count under 45 and 70 pounds extra CO_2 pressure up to ten days. *Bact. typhosum* increased in numbers under low (45 pounds) pressure. Complete sterility was evidently not reached within 30 days, when 20 organisms per cc. were inoculated into ginger ale.

Hunziker (1924) reported his experiments concerning the effect of carbon dioxide on butter. Two lots of butter were churned experimentally on a commercial scale. One-half of the cream was given carbon dioxide treatment. No bacterial counts are given, but the examination showed that the carbonated butter had turned rancid, and the score dropped from 89 points (fresh butter) to 83 points at the end of 12 weeks. This would indicate that carbonation cannot be relied upon to prevent bacterial deterioration of butter.

Prucha, Brannon and Ruehe (1925) concluded that if any appreciable benefit is to be expected from the carbonation of butter, it is necessary to store the butter in an atmosphere of CO_2 in an air tight container.

EFFECT ON BACTERIUM ABORTUS

Theobald Smith (1924) reported studies with *Bact. abortus*, which had extended over a period of two years. It is noteworthy to observe that freshly isolated strains yielded better growth under CO_2 than under ordinary atmosphere. According to him, certain strains may not develop at all in the open culture tube. It was found, further, that by removing the CO_2 with sodium hydrate, growth is inhibited completely in freshly isolated strains, and materially retarded in old strains. It developed further that as high as 100 per cent carbon dioxide could be tolerated by the organism. There was, however, some retardation of growth. Growth of certain strains appeared in eleven day old tubes, under carbon dioxide, which had shown no indications of development under ordinary atmospheric conditions. The author suggests that further studies may show that *Bact. abortus* (Bang) is the only pathogenic organism which possesses such a CO_2 relationship. It is further pointed out that the different strains of *Bact. abortus* fall into two groups, parasitic and saprophytic. In a later work (1926) the same writer stated that this relationship to CO_2 may serve a useful purpose in differentiating *Bact. abortus* strains into the bovine type on the one hand, and the so-called vaccinal or persistent udder strains on the other.

Rockwell (1924) advocated the use of carbon dioxide in anaerobic cultures, and presented experimental evidence of successful cultural work by this method, with *Cl. welchii*, *Cl. tetani*, an organism from chronic bronchitis, and with *Cl. botulinum*.

Sierakowski and Zajdel (1924), discussing the rôle of carbon dioxide in hermetically sealed bacterial cultures, observed that this gas adjusts the final H-ion concentration to pH 6.8. This they claimed to be true in all bacterial cultures. Evidence to this effect was offered for *B. dysenteriae* (Flexner), *Bact. typhosum*, *Bact. paratyphosum* A, B, and C, *Bact. coli*, *V. cholerae*, *C. diphtheriae*, *Prot. vulgaris* and *Staphylococcus*. Five day old cultures, when stoppered, do not acidify, that is reach a pH of 6.8, since these are evidently dying off and do not produce CO_2. According to them, production of CO_2 may be taken as an indication of viability in a culture.

Novy and Soule (1925) arrived at the conclusion that *M. tuberculosis* does not require CO_2 for its development, and that it is not inhibited, therefore, by the removal of carbon dioxide from the cul-

ture. Whatever inhibition has been observed by earlier workers and by Novy and Soule under certain conditions was, according to them, entirely due to desiccation. This conclusion was challenged, however, by Rockwell and Highberger (1926), who confirm Wherry's former findings that *M. tuberculosis* cannot develop without carbon dioxide and that the inhibitive effect is not due to desiccation. It was shown that with as much as 40 per cent dehydration (by sulphuric acid) growth was as good as in the control tube.

In the realm of autotrophic bacteria, Waksman and Starkey (1922–23) and Starkey (1925) have shown that the sulphur oxidizing bacillus, *Thiobacillus thiooxidans*, requires and utilizes carbon dioxide in a manner similar to the nitrifying organisms.

Masur (1926) reported that he was able to cultivate a strain of tubercle bacillus for sixteen generations in a medium containing no carbon except the carbon dioxide of the air. An experiment was also described which indicates that this organism will not develop in the absence of free carbonic acid gas. The investigator concludes that "under certain conditions the tubercle bacillus can utilize directly the carbon dioxide of the atmosphere."

Kulp (1926) based his method of determining the viability of *L. acidophilus* on the principle recently announced by Valley and Rettger (*vide infra*) that carbon dioxide is necessary for bacterial development. Carbonic acid gas, ten per cent by volume, is supplied to the agar plates in a special closed container. Considerably higher viability counts are obtained in this manner than by the customary open method. Furthermore, the colonies are also larger and, as a rule, more characteristic.

INHIBITION OF BACTERIAL GROWTH IN ABSENCE OF CARBON DIOXIDE

Valley and Rettger (1925, 1926, 1927) studied a large number of bacterial species and individual strains and their response (1) to high concentrations of carbon dioxide, and (2) to complete carbon dioxide removal from the environment. From their studies it is evident that the inhibiting effects observed with high concentrations of carbon dioxide (30 to 100 per cent) are primarily, and in many instances entirely, due to increased H-ion concentration of the medium. Displacement of oxygen from the environment by the large amounts of CO_2 gas is often a factor also. They have found, on the other hand, that bacterial growth is inhibited by the complete removal of carbon dioxide from the cultural environment. Under carbon dioxide-free, but otherwise favorable conditions, many of the organisms employed were actually killed in 24 to 48 hours, presumably as the result of complete inanition. A total of 109 different organisms were studied, the selection comprising several important representatives of the various bacterial groups. These authors found that the minimum CO_2 requirement for the various groups or species varied within wide limits.

The findings of Valley and Rettger were corroborated by Rockwell and Highberger (1927), who reported that *Bact. coli*, *Pr. vulgaris* (*B. proteus*), *Ps. pyocyanea* and *Staph. albus* were inhibited in their growth by the removal of carbon dioxide from the environment. The latter investigators also showed that a strain of yeast (*Saccharomyces*) and a strain of mold (*Mucor*) were likewise inhibited by the removal of carbon dioxide.

Rippel and Bortels (1927) have shown that *Aspergillus niger* spores germinate very poorly when cultivated under CO_2-

free conditions. This recent observation is in full accord with that of Durrell (1924), namely that the spores of *Basisporum gallarum* do not germinate in the absence of carbon dioxide, and are in turn stimulated by small amounts of added CO_2 gas.

Phelon, Duthie and McLeod (1927) attempted to employ oxygen-carbon dioxide mixture for the aeration of meningococcus cultures. Their object was to prevent extreme alkalization of the culture. With a gas mixture containing 20 per cent carbon dioxide it was possible to maintain the culture fluid at pH 7.0 and to prolong the life of the culture slightly beyond that of the control, which was aerated with an oxygen nitrogen mixture.

Plastridge and Rettger (1927) have employed gaseous carbon dioxide for aeration purposes in experimental diphtheria toxin production. In cultures which were grown in an atmosphere enriched with 3 per cent carbon dioxide highly potent toxin was produced with regularity. Deterioration of the toxin was prevented in the original culture, even during several weeks of continued incubation. These authors have since found that the filtered toxin is stable under CO_2 at various temperatures of storage. It was further observed that the culture of *C. diphtheriae* under increased carbon dioxide tension contained many more viable organisms than those grown under the usual conditions. The initial H-ion concentration was fairly evenly maintained during the incubation, by passing a slow stream of ordinary air containing from 3 to 5 per cent of added carbon dioxide over the culture.

CONCLUSIONS

In this review, the investigations dealing more or less with the effects of carbon dioxide on bacteria are given in chronological sequence. According to subject matter, they could be grouped as follows:

(1) Those that were concerned with the destructive action of CO_2 on bacteria, pro and con. The period covered here extends approximately from 1877 to 1915, though some work on this phase has appeared as late as 1924, or even later.

(2) Those investigations which deal with the beneficial influence of carbon dioxide, also pro and con. The beginning of this second period was probably signalled by Nowak's partial-tension method for the cultivation of *Bact. abortus* (Bang) in 1908, but more definitely in 1916, with Wherry and Oliver's contribution to the study of the gonococcus, although still under the conception of the partial tension idea. Chapin (1918) applied gaseous CO_2 in the cultivation of the gonococcus, and Cohen and Fleming employed this gas in the primary cultivation of the meningococcus.

(3) Studies concerned with carbon dioxide as a definite requirement. The conception that CO_2 may be necessary or absolutely essential to bacterial growth has been very gradual in its development. Vinogradsky (1890) proved that CO_2 is necessary for the nitrifying bacteria. Lieske (1911) found the same to be true for *Spirophyllum ferrugineum*. Wherry and Ervin (1918) were the first apparently to recognize this requirement for the tubercle bacillus, and their observations were later confirmed by Rockwell and Highberger. Theobald Smith (1924) observed that CO_2 is necessary for *Bact. abortus*, since the organism failed to grow in the presence of sodium hydrate. Valley and Rettger (1925, 1926, 1927) reported that complete inhibition of growth of common laboratory stock cultures had been obtained by CO_2 exclusion, and that CO_2 is necessary for bacterial development.

It will be seen from the above review that experimental evidence concerning the effect of carbon dioxide on bacteria has been accumulating during the past fifty years. The efforts of the earlier workers were for the most part directed to a study of the inhibitive action of carbon dioxide on bacterial growth.

Gradually another line of evidence has been accumulating. It has become more and more apparent that this agent, though it exerts a harmful influence on bacteria under certain conditions, may be of supreme importance, whether directly or indirectly, in their economy. The application of added carbon dioxide gas in the primary cultivation of the so-called partial tension organisms (*Bact. abortus* and *L. acidophilus*, for example) furnishes ample evidence to support this view.

Finally, observations of the past five or six years have brought forward the conception that carbon dioxide as such is necessary for bacterial growth and development, and therefore, for life itself. This conception rests on experimental evidence obtained with various bacterial species, particularly by Valley and Rettger, who found that of 109 different organisms employed in their carbon dioxide studies none could be made to develop in otherwise favorable culture media when they were deprived of all carbon dioxide.

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THE EVOLUTIONARY SIGNIFICANCE OF THE PROTOZOAN PARASITES OF MONKEYS AND MAN

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INTRODUCTION

PARASITISM is one of the many types of association that exist between different species of living organisms. When used in a narrow sense the term implies injury to one member of the association, the host, and benefit to the other, the parasite; but as generally employed the term parasite is given to any animal or plant that lives on or within and at the expense of another animal or plant. Such associations are, at least in some instances, actually beneficial to the host, as Cleveland (1926) has shown in the case of termites (white ants) and their intestinal flagellates. The latter digest the cellulose in the wood eaten by the termites, thus making it available for the nourishment of these insects; otherwise the termites would starve to death in the midst of an abundance of food. Many groups in the animal kingdom contain parasitic species, and the evidence is overwhelmingly in favor of the view that the parasitic habit has evolved from the free-living mode of existence and has arisen many times within each group. Parasites are particularly abundant among the Protozoa, flat worms (Platyhelminthes), round worm (Nemathelminthes), and Arthropoda (insects and arachnids).

Protozoa and Primates belong to the first and last phyla in the animal kingdom when these are arranged in an evolutionary series. Both groups have been very successful in the struggle for existence, since one of the primates, Man, is now the dominant species on the surface of the earth, and the Protozoa probably excel in number of species and in number of individuals every other group of animals. These two types of animals are not only able to live and reproduce under the complex conditions that now exist in the world, but many of them live together as parasite and host. The results of this type of parasitism are often beneficial to the protozoa and may or may not be harmful to the primates.

The monkeys and man are included in the order Primates in the Class Mammalia. One difficulty in any discussion of the primates is that of nomenclature; so many common and scientific names have been proposed for the various species that much confusion exists and it is often impossible to determine which species is being referred to. The large *Review of the Primates* by Elliot (1913) is not very satisfactory from the standpoint of classification but is used as a basis by many writers. Recently Stiles and Orleman (1927) have prepared a bulletin on *The Nomenclature for Man, the Chimpanzee, the Orang-utan, and the Barbary Ape*, and the names of the other primates that are known to be parasitized by Protozoa are soon to be presented according to modern methods of nomenclature in another

bulletin. In the meantime the writer has used the scientific and common names employed in the current literature.

The Protozoa are usually separated into four classes, the members of which can be distinguished by the presence or absence of locomotor organs and the character of these when present. The Sarcodina throw out temporary cytoplasmic projections known as pseudopodia; the Mastigophora possess one or several threadlike flagella; the Sporozoa have no locomotor organs; and the Infusoria are covered more or less completely with minute hair-like cilia. The Sporozoa are all parasitic, but the other three classes include both free-living and parasitic species. Protozoa are all very small; a few of them can be seen with the naked eye, especially when large numbers are crowded into a small area, but most of them are microscopic in size. Elaborate methods have been evolved during the course of years for their study, and it is now possible to cultivate not only free-living species, but also many of the parasitic forms, in test tubes in artificial media. Much has been learned by the use of laboratory animals; and cross-infection experiments have revealed many data regarding the environmental factors necessary for their growth and reproduction.

Both monkeys and man are parasitized by certain members of all four classes of Protozoa. For convenience we may recognize two types of protozoan parasites, (1) intestinal protozoa, including also those that live in the mouth, stomach, vagina, and urinary tract, and (2) blood-inhabiting protozoa. The former include representatives among the amoebae (figs. 1–4), flagellates (figs. 5–9), coccidia and ciliates (figs. 10–11). Many protozoa have been described from human fecal material that are not inhabitants of the intestine but were either ingested in food or drink and had passed through the digestive tract in a viable condition, or had found their way into the feces after they were passed: these are known as coprozoic protozoa. The blood-inhabiting protozoa of primates consist principally of certain flagellates (figs. 12–13) and malarial organisms (figs. 14–19). Besides the protozoa belonging to the two large groups mentioned, are the sarcosporidia (Sporozoa) that parasitize muscle, and a few others of doubtful validity.

One of the most fascinating problems in protozoology is that of host-parasite specificity (Hegner, 1926a). Why is it that one species of protozoon is able to live in one species of animal but not in another nearly related species? This appears to be true of most species of human parasites. Does the ability of a protozoon to live in two species of animals indicate that the latter are closely related? This is a problem of great interest and importance, since evidence of the organic evolution of hosts may be inferred from the character of their parasites. It is mainly with this point in mind that this article has been prepared. A comparison is presented in the following pages of the amoebae, intestinal flagellates, intestinal ciliates, trypanosomes, leishmanias, malarial parasites, and certain other species of protozoa that live in monkeys and man. This requires the use of many scientific names, both of the protozoa and of their monkey hosts; but the accompanying figures may serve to make these intelligible to readers who are not biologists. This is followed by a brief résumé of the species that occur in the two types of hosts, and is concluded with a statement regarding the significance of these parasites in the study of genetic relationships of hosts as applied to monkeys and man.

Hundreds of different species of intestinal protozoa have been reported from man, but careful study indicates that most of these are not separate species. On the basis of our present knowledge we may recognize six species of amoebae (Sarcodina), seven species of flagellates (Mastigophora), one species of coccidium (Sporozoa), and one species of ciliate (Infusoria). All of these protozoa appear to be world wide in their distribution, and no differences as regards racial susceptibility have been established with certainty; resistance of the individual, however, appears to increase with age. The location of these species in the body and the approximate incidence of infection among the general population are as follows:

	per cent
Mouth:	
Endamoeba gingivalis (Amoeba)	50
Trichomonas buccalis (Flagellate)	10–30
Small intestine:	
Giardia lamblia (Flagellate)	10
Isospora hominis (Coccidium)	?
Large intestine:	
Endamoeba histolytica (Amoeba)	10
Endamoeba coli (Amoeba)	50
Endolimax nana (Amoeba)	25
Iodamoeba williamsi (Amoeba)	10
Dientamoeba fragilis (Amoeba)	?
Trichomonas hominis (Flagellate)	5–20
Chilomastix mesnili (Flagellate)	10
Embadomonas intestinalis (Flagellate)	?
Tricercomonas intestinalis (Flagellate)	?
Balantidium coli (Ciliate)	?
Vagina and urinary tract:	
Trichomonas vaginalis (Flagellate)	10–50 (in women)

Two points of particular interest brought out by these data are the high incidence of infection with certain species and the differences in incidence among the various species. It is evident that man is very susceptible to infection with such species as *Endamoeba gingivalis*, *Trichomonas buccalis*, *Endamoeba coli*, and *Trichomonas vaginalis*. It is also obvious that these species have little difficulty in gaining entrance to the human body. The two species that inhabit the oral cavity are no doubt frequently passed from mouth to mouth during kissing, and probably no one escapes contamination with these protozoa. The intestinal species are mostly transmitted in the cyst stage and the high incidence of infection indicates that contamination of food and drink with feces containing cysts is frequent and widespread.

The facts regarding the pathogenicity of human intestinal protozoa may be stated briefly as follows. *Endamoeba histolytica* is pathogenic especially in tropical and semitropical regions; it is the etiological agent of amoebic dysentery and amoebic liver abscess, and is frequently fatal. Most of those infected with this species are carriers and do not exhibit symptoms. *Endamoeba coli* and *Endamoeba gingivalis* may be pathogenic but this has not yet been definitely proven. The other species of amoebae appear to be harmless. Of the flagellates, *Giardia lamblia*, *Trichomonas hominis*, and *Chilomastix mesnili*, have been accused of causing "flagellate diarrhea;" but their actual relation to the diarrheic condition is not certain; *Trichomonas buccalis* seems to be more frequent in persons suffering from pyorrhea, acute gingivitis, or abscessed teeth than in normal mouths (Hogue, 1926; Hinshaw, 1926), but are probably not responsible for these diseases; *Trichomonas vaginalis* is more common when the vaginal mucus is in an abnormal condition but its relation to the host is still uncertain; the other

species of flagellates are both rare and apparently harmless. The human coccidium, *Isospora hominis*, is always pathogenic but is rare and the diarrhea it produces is of short duration and not lethal. The ciliate, *Balantidium coli*, is the agent of balantidial dysentery, which may be fatal to the host, but is not of frequent occurrence.

The blood-inhabiting protozoa of man are three species of trypanosomes (Mastigophora), three species of leishmanias (Mastigophora), and three species of malarial parasites (Sporozoa). These are all pathogenic and of great importance where they occur, but are more or less local in their distribution. The trypanosomes cause Gambian sleeping sickness (*Trypanosoma gambiense*) and Rhodesian sleeping sickness (*T. rhodesiense*) in tropical Africa, and Chagas' disease (*T. cruzi*) in certain parts of South America. The leishmanias cause kala-azar (*Leishmania donovani*) in parts of Asia, Africa and Europe, oriental sore (*L. tropica*) in certain regions of Asia and Africa, and South American leishmaniasis (*L. braziliensis*) in South America. The three species of malarial parasites, *Plasmodium vivax* of tertian malaria, *P. malariae* of quartan malaria, and *P. falciparum* of estivo-autumnal malaria, occur in tropical and semitropical regions throughout the world.

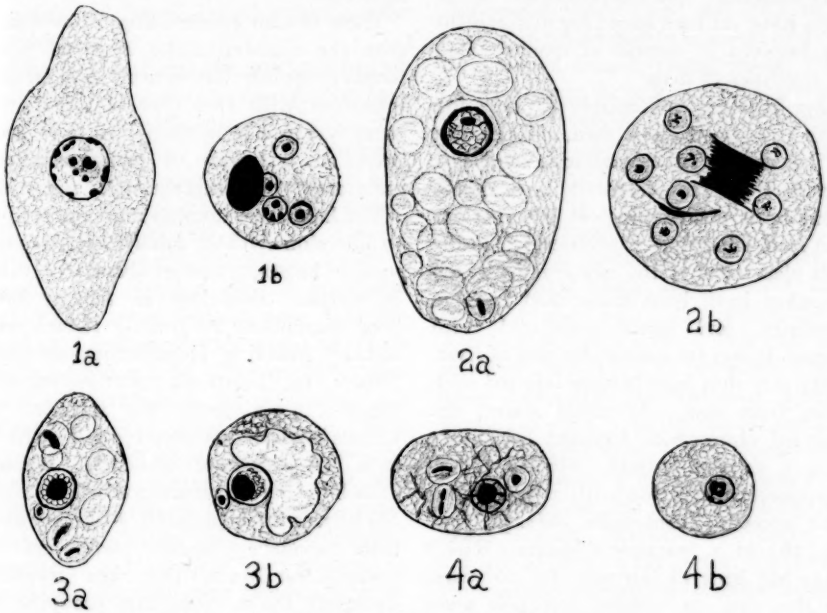
Protozoa were first discovered in man by Leeuwenhoek in 1681. Among the many protozoa described by this famous Dutch microscopist were flagellates, that we now know as giardias, which he encountered in his own stools. However, free-living species were the first to receive attention from biologists, and only comparatively recently have parasitic species attracted investigators. Such discoveries as that of the parasite of amoebic dysentery by Loesch in 1873 (Loesch, 1875), of the malarial parasite by Laveran in 1880 and of a human trypanosome by Forde in 1901 (Forde, 1902) stimulated thousands of investigators to enter the field of protozoology and has resulted in a large body of knowledge regarding the parasitic species, especially those that live in man and domesticated animals.

Protozoa were first reported from monkeys about the year 1899 when Laveran named a species of malarial parasite, *Plasmodium kochi*, that Koch had discovered in 1898 in Africa. Trypanosomes were noted in the chimpanzee by Ziemann in 1902; the ciliate, *Balantidium coli*, in orang-utans by Brooks in 1903; amoebae in a macaque, *Macacus pileatus*, by Castellani in 1908; and intestinal flagellates in another species of macaque, *Macacus cynomolgus*, by Noc in the same year. During the succeeding twenty years protozoa resembling almost every species known to live in man have been recorded from monkeys. It was not, however, until about 1920 that investigators attempted to determine by experiment whether the protozoa of monkeys and man belong to the same or to different species. Recently many cross-infection and cultivation experiments have been carried out, but we are still very much in doubt regarding the host-parasite specificity of monkey protozoa.

AMOEBAE OF MONKEYS AND MAN

At least eleven species of amoebae belonging to three genera have been described from monkeys. Nine of these have been placed by their discoverers in the genus *Endamoeba* and one each in the genera *Endolimax* and *Iodamoeba*. The endamoebae all fall into two types that correspond to two of the common species living in man, namely, *Endamoeba coli* with cysts containing 8 nuclei (fig. 2b), and *E. histolytica* with cysts possessing

4 nuclei (fig. 1b). *Endamoeba nuttalli* of Castellani (1908) resembles *E. histolytica* of man both in the active trophozoite stage and in the character of its cysts. It seems probable that if *E. nuttalli* is a species distinct from *E. histolytica*, then of Old World and New World monkeys. The amoebae to which Castellani gave the name *E. nuttalli* were found by him in a liver abscess in a macaque (*Macacus pileatus*) in Colombo, Ceylon; and Suldey (1924) reported typical amoebic dysentery



AMOEBAE OF MONKEYS AND MAN

FIG. 1a. *Endamoeba duboscqi*. Active, trophozoite stage of histolytica-type o amoeba from the rhesus monkey, *Macacus rhesus*. (After Mathis.)
FIG. 1b. *Endamoeba duboscqi*. Cyst stage containing four nuclei and large chromatoid body. (After Mathis.)
FIG. 2a. *Endamoeba pitheci*. Active, trophozoite stage of coli-type of amoeba from a monkey. (After Hegner and Taliaferro.)
FIG. 2b. *E. pitheci*. Cyst stage containing eight nuclei and chromatoid bodies. (After Hegner and Taliaferro.)
FIG. 3a. *Iodamoeba kueneni*. Active, trophozoite stage from a monkey resembling similar stage of *Iodamoeba williamsi* of man. (After Hegner and Taliaferro.)
FIG. 3b. *Iodamoeba kueneni*. Cyst stage from a monkey. (After Hegner and Taliaferro.)
FIG. 4a. *Endolimax nana*. Active, trophozoite stage from man. (After Hegner and Taliaferro.)
FIG. 4b. *Endolimax nana*. Cyst stage from man. (After Hegner and Taliaferro.) All figures drawn at a magnification of about 2000 diameters.

the other four species described from monkeys belong to that species (*E. nuttalli*). These histolytica-like amoebae have been noted in the gorilla (Wenyon, 1926), chimpanzee (Suldey, 1924; Deschiens, 1927), and various other species in a three year old captive chimpanzee. Most of the infected monkeys, however, appear to be carriers, that is, the amoebae are present in the intestine, where they grow, multiply and form cysts, but the host-parasite relations are such that symp-

toms do not appear. In these respects this type of monkey amoeba resembles *E. histolytica* of man; the latter is present in about ten per cent of healthy human beings in the general population but occasionally gives rise to dysentery and liver abscesses. No morphological differences have yet been found for distinguishing between *E. nuttalli* of monkeys and *E. histolytica* of man.

Are monkeys susceptible to infection with *E. histolytica* from man, and can man be infected with *E. nuttalli* from monkeys? Evidence on cross-infection is available from both epidemiological observations and from laboratory experiments. In the first place most of the monkeys in which amoebae have been found had been in captivity, and hence associated with human beings for various lengths of time. They may thus have become infected with cysts from man. As noted above, the infected chimpanzee reported by Suldey was a captive animal. Mathis (1913) described an infection with a histolytica-like amoeba (*Endamoeba duboscqi*, figs. 1a, 1b) in a macaque (*Macacus rhesus*) that had been in Germany for 16 years; in this case an original infection must have lasted for that length of time or else the monkey became infected with human amoebae while in captivity, or possibly with amoebae from other monkeys with which it was associated. On the other hand, McCarrison (1919), as a result of studies on 36 young monkeys (*Macacus sinicus*) in India, states that "monkeys in a wild state in S. India may be carriers of *E. tetragena* (*histolytica*)." Successful attempts to infect monkeys by inoculating them with trophozoites or cysts of *E. histolytica* from man have been reported by several investigators. Thus Franchini (1912) claims to have infected a monkey (species not given) with *E. histolytica* per rectum. Kessel (1926a) fed cysts of *E. histolytica* to two amoeba-free monkeys (*Macacus*) and recovered trophozoites and cysts from their feces racially indistinguishable from the type of amoebae fed to them, and, after autopsy, found similar specimens in histological sections.

There is also epidemiological evidence that the histolytica-like amoebae from monkeys are infective to man; for example, infections with this type of amoeba in three individuals in Baltimore have been traced to a colony of rhesus monkeys maintained for experimental purposes.

The laboratory animals most susceptible to infection with *E. histolytica* from man seem to be young cats of about 500 grams in weight. Infections in kittens have been established by feeding them cysts, and by injecting trophozoites or cysts (Hoare, 1925) into the colon per rectum. Mello (1923) reports the infection of kittens by the rectal injection of dysenteric feces of monkeys (*Macacus sinicus*). Dobell (1926) likewise succeeded in infecting kittens with histolytica-like amoebae from monkeys (*Macacus rhesus* and *M. sinicus*) but states that the resulting dysentery differs from that produced by *E. histolytica* from man. The infection of two cats, 6 and 7 months old respectively, by rectal injections of feces containing cysts of naturally infected monkeys was obtained by Kessel (1926a). Two months after injection the cats at autopsy were found to contain trophozoites in the upper colon and cecum and also in the tissues of the intestinal wall. In a later paper Kessel (1927) reports the successful infection of 8 of 13 kittens with trophozoites or cysts of histolytica-like amoebae from monkeys; 6 of the kittens succumbed to dysentery of the type induced in these animals by *E. histolytica* from man.

The methods introduced by Boeck and Drbohlav (1925) for cultivating human

amoebae have also been used for the cultivation of amoebae from monkeys. Dobell (1926, 1927) has carried on cultures of the histolytica-like amoebae of monkeys for many months and finds no differences between their reactions in culture and those of *E. histolytica* from man. Kessel (1926a) and Vogel (1927) report similar results.

The data available lead to the following conclusions regarding *Endamoeba histolytica* from man and the histolytica-like amoebae from monkeys: (1) The histolytica-like amoebae of monkeys, which have been given at least five distinct specific names, all belong, probably, to one species, *Endamoeba nuttalli* Castellani 1908, if they are not identical with *E. histolytica*. (2) There are no satisfactory morphological characteristics by means of which the histolytica type of amoebae of monkeys and man can be distinguished. (3) Histolytica-like amoebae have been reported principally from captive monkeys that may have become infected by the ingestion of food or drink contaminated with cysts from man. (4) Amoebic dysentery and amoebic liver abscess in monkeys resemble these diseases in man. (5) Most monkeys and men infected with histolytica amoebae are carriers. (6) Monkeys have been successfully infected with *E. histolytica* from man. (7) Human beings seem to have become infected by association with monkeys. (8) Kittens may be infected by amoebae from both monkeys and man. (9) Histolytica amoebae from monkeys and man exhibit similar reactions under cultivation in artificial media. (10) Either the histolytica-like amoebae of monkeys belong to the species *Endamoeba histolytica* or else we have not yet discovered differences sufficient to distinguish one from the other.

The situation as regards *Endamoeba coli* of man and the coli-like amoebae of monkeys is similar to that of *E. histolytica*, but not so much evidence is available. Brumpt, in 1909, reported amoebae with eight-nucleated cysts from three specimens of *Macacus sinicus*. Three years later, Prowazek (1912) gave the name *Endamoeba pitheci* (figs. 2a, 2b) to an amoeba with an eight-nucleated cyst that he obtained from a young orang. New specific names have since been given to three other coli-like amoebae found in other species of monkeys (Mathis, 1913; Macfie, 1915; Mello, 1923). There is little evidence that these are actually separate species, and they probably all belong to the species *E. pitheci* if they are not identical with *E. coli* from man. Kessel (1924, 1927) has succeeded in infecting monkeys with *E. coli* from man and both Dobell (1926) and Kessel (1927) have cultivated the coli-like monkey amoeba in vitro. At the Pasteur Institute in Paris, Deschiens (1927) found coli-like amoebae in 5 of 7 chimpanzees and successfully infected a young chimpanzee and a *Macacus* monkey with them; his attempt to infect a cat proved negative as did a similar attempt by Brumpt (1909b). Apparently, therefore, there is no good evidence that the coli-like amoebae of monkeys differ in species from *E. coli* in man.

Amoebae of the genus *Endolimax* (figs. 4a, 4b) have been reported from monkeys by only two investigators. Brug, in 1923, found in an old laboratory monkey (*Macacus cynomolgus*) an amoeba morphologically identical with *Endolimax nana* from man, to which he gave the name *Endolimax cynomolgi*. The second record is that of Deschiens (1927) who reported it from 3 of 7 chimpanzees, from 2 of 9 macaques, and from 2 *Cercopithecus* monkeys at the Pasteur Institute in Paris. He transferred the infection from chim-

panzees to macaques and from one macaque to another. Infections in monkeys with *Endolimax nana* from man have been reported by Kessel (1927). From these meager data it seems possible and even probable that the *Endolimax* of monkeys and man are of the same species.

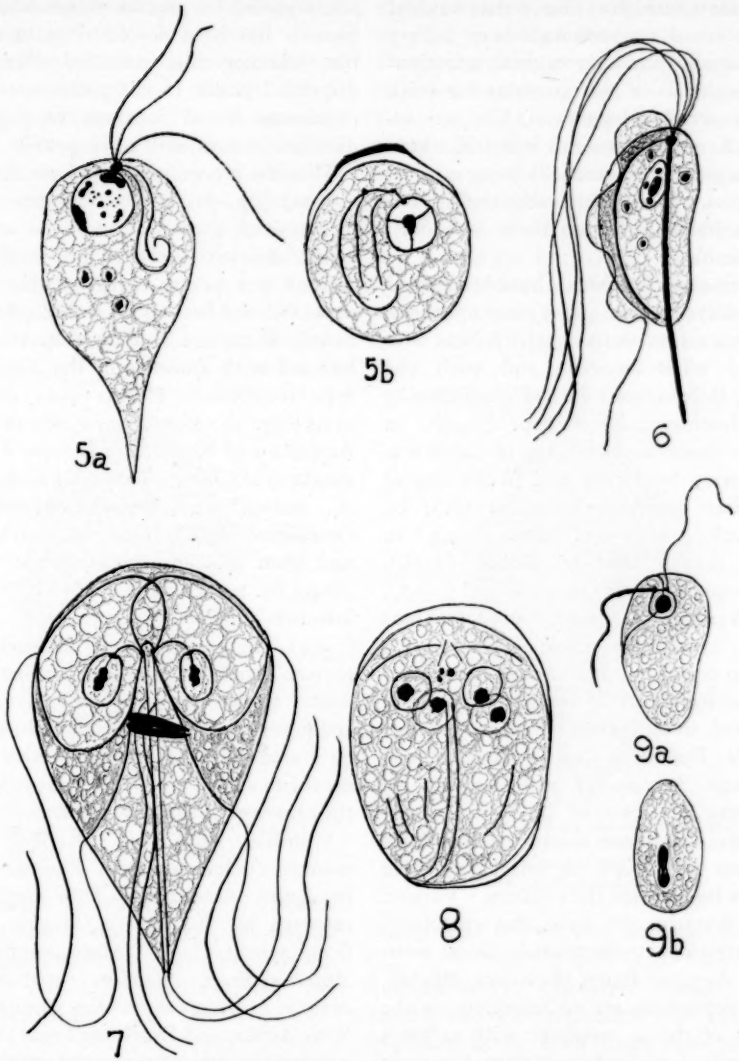
Iodamoebae (figs. 3a, 3b) were first noted in monkeys (*Macacus cynomolgus*) by Brug in 1921; he believed them to be *Endolimax* and gave them the specific name *kueneni*, but his descriptions and figures indicate that they belong to the genus *Iodamoeba*. Since then iodamoebae have been reported from monkeys by Hegner and Taliaferro (1924, in *Cebus variegatus*), Kessel (1924, 1927, in *Macacus*), Wenyon (1926, in the gorilla) and Smith (1928, in *Macacus rhesus*). Recently specimens were found in the writer's laboratory in the intestine of a chimpanzee. Kessel (1924) claims to have infected both of two *Macacus* monkeys with cysts of *Iodamoeba* from man, and Smith (1928) could find no differences between excystation in iodamoebae from man and from *Macacus* monkeys when cysts were fed to guinea-pigs. Brug (1921) states that the cysts of *Iodamoeba kueneni* possess a darkly staining area not present in cysts from man, but it does not seem probable that this characteristic is constant. As in the case of *Endolimax* the conclusion is reached that the iodamoebae of monkeys and man have not yet been shown to belong to different species.

Two species of amoebae that live in man have not yet been reported from monkeys so far as known to the writer. These are *Endamoeba gingivalis*, which inhabits the mouth, and *Dientamoeba fragilis* of the intestine. Smears and cultures from the mouths of many monkeys have been examined in the writer's laboratory for *E. gingivalis* but without success. *Dientamoeba fragilis* is rare in man and may probably live in monkeys but has not been found thus far. Kessel (1924) claims to have found in *Macacus* monkeys amoebae indistinguishable from *Councilmania lafleuri*, a form that Kofoid and Swezy (1921) described as a new genus and species from man but that is believed by many protozoologists to be *Endamoeba coli*, and reports the successful infection of two monkeys with cysts of *C. lafleuri* from man. None of the other doubtful species of amoebae that have been described from man have been encountered in monkeys.

INTESTINAL FLAGELLATES OF MONKEYS AND MAN

Of the seven species of intestinal flagellates that live in man three belong to the genus *Trichomonas* and the other four to the genera *Chilomastix*, *Giardia*, *Embadomonas*, and *Tricercomonas*. An eighth species of doubtful validity is *Enteromonas hominis*. The trichomonads, *Chilomastix*, and *Giardia* are relatively common (see page 227), whereas *Embadomonas* and *Tricercomonas* are rare. Representatives of all of these genera, with the exception of *Tricercomonas*, have been reported from monkeys. The trichomonads of man occur in the intestine (*Trichomonas hominis*), in the mouth (*T. buccalis*) and in the vagina (*T. vaginalis*). Intestinal and vaginal trichomonads occur in monkeys, but the mouth inhabiting type has not been found, although thorough search has been made for it in the writer's laboratory.

Vaginal trichomonads have been reported from monkeys only once (Hegner and Ratcliffe, 1927); these were given the name *Trichomonas macacovaginae* (fig. 6). Trichomonads from the intestine of *Macacus* monkeys when grown in culture and injected into the vagina of uninfected monkeys appeared in 4 of 6 cases to set up at least temporary infections. These



INTESTINAL FLAGELLATES OF MONKEYS AND MAN

FIG. 5a. *Chilomastix mesnili*. Active, trophozoite stage from man. (After Hegner.)
FIG. 5b. *Chilomastix* sp. Cyst stage from a monkey. (After Hegner.)
FIG. 6. *Trichomonas macacovaginae*. Active, trophozoite stage from the vagina of a monkey. (After Hegner and Ratcliffe.)
FIG. 7. *Giardia lamblia*. Active trophozoite stage from man. (After Hegner.)
FIG. 8. *Giardia* sp. Cyst stage from a monkey. (After Hegner.)
FIG. 9a. *Embadomonas intestinalis*. Active, trophozoite stage from man. (After Hegner and Taliaferro.)
FIG. 9b. *Embadomonas intestinalis*. Cyst stage from man. (After Hegner and Taliaferro.) All figures drawn at a magnification of about 4000 diameters.

experiments furnish evidence that vaginal and intestinal trichomonads may belong to one species and that vaginal infections are brought about by contamination with fecal material (Hegner, 1928). No attempts have been made to infect monkeys with vaginal trichomonads from man or vice versa. Morphologically the trichomonads from these two hosts are indistinguishable.

Intestinal trichomonads have been noted in monkeys by Noc (1908) in a specimen of *Macacus cynomolgus*, which was also infected with amoebae and with the ciliate, *Balantidium coli*, and was suffering from dysentery; by Brumpt (1909b) in *Macacus sinicus* monkeys, one of which was dysenteric; by Greig and Wells (1911) in Indian monkeys (*Macacus* sp.); by Prowazek (1912) and Mello (1923) in young orangs; and by Dobell (1926), Hegner and Ratcliffe (1927), Kessel (1927), Branch and Gay (1927), and Deschiens (1927). Although these trichomonads seem to possess no morphological characteristics by means of which they can be separated from human intestinal trichomonads, Deschiens (1927) has proposed the name *Trichomonas anthropopitheci* for specimens he observed in captive chimpanzees. Deschiens cultivated this form in vitro but failed to infect a human being who ingested the cultures. Various other investigators have also cultivated the intestinal trichomonads from monkeys. As noted above, the writer (Hegner, 1928) apparently set up infections in the vagina of rhesus monkeys with cultures of intestinal trichomonads from the same species of host. Kessel (1924) claims to have infected one of two monkeys by feeding them human intestinal trichomonads, and also infected kittens by mouth and by rectum with intestinal trichomonads from both man and monkeys (Kessel, 1926b, 1927). Diarrhea accompanied by great numbers of trichomonads has been described in monkeys, but whether this so-called "flagellate diarrhea" is due to the presence of these organisms is, as in cases of flagellate diarrhea in man, still to be proved.

The first report of *Chilomastix* (=*Macrostoma*) (fig. 5a) from a monkey is that of Prowazek (1912), who found it along with amoebae and trichomonads (see above) in a young orang. Bach (1923) next observed both cysts and trophozoites in an old captive monkey that was also infected with amoebae of the histolytica type (see above). Hegner (1924) reported cysts (fig. 5b) from *Cebus apella* of South America and Kessel (1924) from *Macacus* monkeys of China. Cysts of a *Chilomastix* (*C. mesnili* var. *simiae*), obtained by Deschiens (1926) from the chimpanzee and from *Macacus sinicus*, when fed to young *M. sinicus* monkeys brought about infection in from 15 to 30 days. Kessel (1924) claims to have infected both of two monkeys by feeding them *Chilomastix* from man. Further observations and experiments are necessary before it can be stated with certainty whether *Chilomastix* from monkeys and man belong to the same or to different species.

Giardias were first described in a monkey (*Cebus caraya*) by Fonseca (1915) in South America. They were next reported by the writer (Hegner, 1924) from another South American monkey, *Ateleus geoffroyi*. Wenyon (1926) observed cysts in a young *Cercopithecus* monkey from West Africa, and Deschiens (1927) records giardias in one *Macacus* and one *Cercopithecus* monkey and succeeded in transmitting them from one macaque to another. Deschiens failed to infect cats with the monkey giardias and Kessel (1924) failed to infect *Macacus* monkeys with giardias from man. These data show that giardias are widespread in monkeys but do not

settle the question of specificity of either parasite or host.

The literature contains two records of *Embadomonas* in monkeys. Fonseca (1917) describes specimens from a South American monkey, *Cebus caraya*, which he considers a new species, *E. wenyoni*, on the basis of differences in the type of division between it and the human form, *E. intestinalis;* that it is a new species seems very doubtful. The second reference is that of Kessel (1927) who found *Embadomonas* in *Macacus* monkeys in China and cultivated them in vitro.

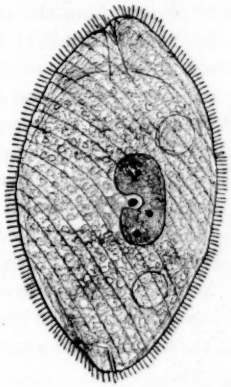


FIG. 10. BALANTIDIUM SP. ACTIVE, TROPHOZOITE STAGE OF CILIATE FROM A MONKEY (×1200)
(After Hegner and Holmes)

Enteromonas is mentioned by Dobell (1926) as one of the intestinal flagellates that he found and cultivated from *Macacus* monkeys, but no description of the organism is given.

INTESTINAL CILIATES OF MONKEYS AND MAN

The only ciliate that is known with certainty to occur in man is *Balantidium coli*. Two genera of ciliates are intestinal inhabitants of monkeys, *Balantidium* (fig. 10) and *Troglodytella* (fig. 11). The balantidia are supposed to belong to the same species as that in man and pig, *Balantidium coli*, and are possibly the same as that in the guinea-pig (Scott, 1927). Two species and one variety of *Troglodytella* have been given names; *T. abrassarti* and *T. abrassarti acuminata* occur in chimpanzees (Brumpt and Joyeux, 1912; Reichenow, 1917, 1920a), and *T. gorillae* in the gorilla (Reichenow, 1920a).

Balantidium coli is a particularly interesting protozoon because its host-parasite specificity seems to be very weak. Apparently human beings acquire infection by ingesting cysts from pigs, a large

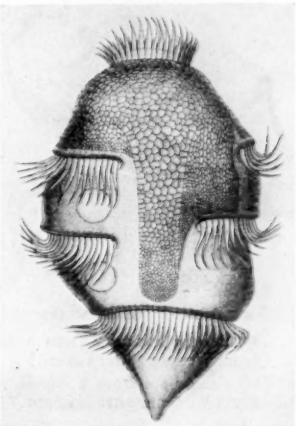
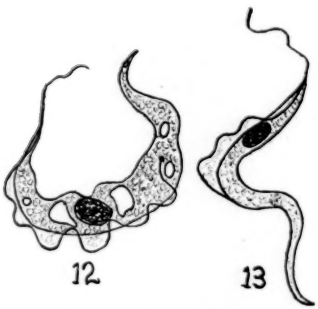


FIG. 11. TROGLODYTELLA ABRASSARTI ACUMINATA. ACTIVE, TROPHOZOITE STAGE OF A CILIATE FROM A CHIMPANZEE (×250)
(After Reichenow)

proportion of which are parasitized. Pigs have been infected with balantidia from monkeys (Brumpt, 1909a); and monkeys have been infected with cysts or trophozoites or both from man or pig when fed to them or injected per rectum (Walker, 1913). Two attempts made by Ziemann (1925) to infect himself by swallowing balantidia from chimpanzees were unsuccessful. Scott (1927) has been unable to find any differences of specific rank between the balantidia of guinea-pigs and those of pig and man.

Balantidia were first reported from monkeys by Brooks (1903) in orangs suffering from dysentery in the New York Zoological Gardens; they have since been found in the baboon (Joyeux, 1913), chimpanzee (Christeller, 1922; Ziemann, 1925) and in other Old and New World monkeys (Noc, 1908; Brumpt, 1909a; Hegner and Holmes, 1923). Cunha and Muniz (1927) have given the name *Balantidium aragãoi* to specimens they describe from *Cebus caraya* of Brazil. In about one-half of the cases reported the infected monkeys were diarrheic or dysenteric; the rest of the infected animals were in the carrier state.



TRYPANOSOMES OF MONKEYS

FIG. 12. *Trypanosoma minasense* from a marmoset (×2000). (From Wenyon, after Carini.)

FIG. 13. *Trypanosoma* sp. from a howler monkey (×2000). (From Wenyon, after Brimont.)

TRYPANOSOMES OF MONKEYS AND MAN

The trypanosomes of man are local in their distribution. *Trypanosoma gambiense* and *T. rhodesiense* occur in certain regions of Africa, where they are responsible for Gambian and Rhodesian sleeping sickness. *T. cruzi*, the organism of Chagas' disease, occurs principally in Brazil, but has been reported also from San Salvador, Venezuela, and Peru. These three species of trypanosomes all have animal reservoirs. Several species of armadillos appear to be natural hosts of *T. cruzi* in South America where as many as 50 per cent of these animals have been found infected; the transmitting agent, the bug, *Triatoma megista*, lives in the armadillo burrows (Chagas, 1918). Antelope and other wild game have been accused of serving as reservoirs of *T. gambiense* and *T. rhodesiense* in Africa in association with the tsetse flies which are the transmitting agents. Man and domestic animals, however, are probably more important reservoirs than wild game. The human trypanosomes can be transmitted by blood inoculation or by means of their transmitting insects to various laboratory animals; among the latter are monkeys. Monkeys have also been reported in endemic regions with what seem to have been natural infections with these three species of trypanosomes. For example, Chagas (1924) found specimens in the monkey, *Chrysothrix sciureus*, of Brazil, which, when inoculated into guinea-pigs and dogs, resembled *T. cruzi* both morphologically and in their effects on these hosts. Various investigators have found trypanosomes in monkeys in Africa that they considered identical with human species.

Trypanosomes (figs. 12, 13) have been reported from over a dozen species of monkeys, including the chimpanzee and gorilla and other Old World and New World species. Some of these monkeys seem to have acquired their infections in a wild state. As many as seven new species or varieties have been described from monkeys, but trypanosomes are not easily distinguishable from one another, and the validity of certain of these new species is in doubt.

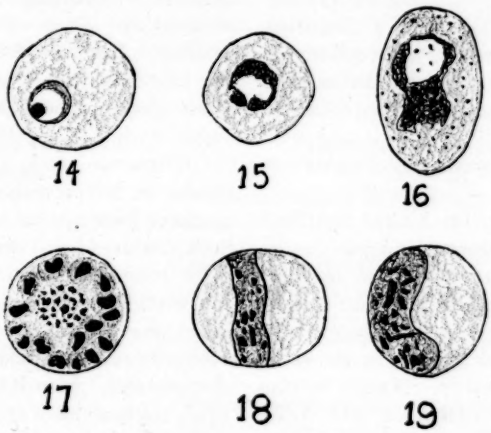
LEISHMANIAS OF MONKEYS AND MAN

The organisms of kala-azar (*Leishmania donovani*), oriental sore (*L. tropica*), and South American leishmaniasis (*L. brazil-*

iense) have not been reported from monkeys. The only natural infections thus far discovered have been in dogs and cats. Laboratory monkeys can be infected by the injection of large doses of *L. donovani* grown in culture, but the virus loses its virulence when passed through a succession of animals and finally becomes noninfective. Monkeys may die after several months as a result of infection with *L. donovani*, or may suffer a chronic infection and recover. In some monkeys, as Row (1912), Korke (1914), and Tyzzer and Walker (1919) have shown, cutaneous inoculation with kala-azar material results in skin lesions and not in generalized infections. Monkeys are also susceptible to infection with both *L. tropica* (Nicolle and Sicre, 1908) and *L. braziliense* (Wenyon, 1913). The organisms bring about the production of lesions that resemble those in man, but disappear sooner.

MALARIAL PARASITES OF MONKEYS AND MAN

Malarial parasites were first found in monkeys by Koch in 1898. During the following year Laveran, the discoverer of the malarial parasites of man, discovered similar organisms in *Cercopithecus sabaeus*, to which he gave the specific name *kochi*. Since then malarial parasites (figs. 14–19) have been reported from the chimpanzee, gorilla, orang, baboon, and over a dozen other species of Old World and New World monkeys. At least eight new species have been described, but how many of these are "good" species is still to be determined. Of particular interest is the fact that certain of these parasites in monkeys resemble so closely the three species that occur in man that they are morphologically indistinguishable. Thus *Plasmodium kochi* (fig. 16) is similar to *P. vivax*, the tertian parasite of



MALARIAL PARASITES OF MONKEYS

FIG. 14. *Plasmodium inui*. Ring stage in red blood corpuscle.
FIG. 15. *P. brasilianum*. Young trophozoite.
FIG. 16. *P. kochi*. Older trophozoite (schizont).
FIG. 17. *P. inui*. Segmentation stage (schizogony).
FIG. 18. *P. malariae*. Band-like stage of trophozoite.
FIG. 19. *P. reichenowi*. Crescent-shaped gametocyte.
All figures drawn at a magnification of about 2000 diameters. (From Wenyon. Figs. 14 and 17 after Mathis and Leger; figs. 15 and 16 after Gonder and Gossler; figs. 18 and 19 after Reichenow.)

man, both in the structure of the various stages and in the length of the asexual cycle (48 hours). Other so-called species that resemble *P. vivax* are *P. inui* (figs. 14, 17) (Halberstädter and Prowazek, 1907) and *P. cynomolgi* (Mayer, 1908) from *Macacus* monkeys, *P. bouilliezi* (Leger, 1922) from *Cercopithecus campbelli*, *P. semnopitheci* (Knowles, 1919) from *Semnopithecus entellus*, and *P. pitheci* (Halberstädter and Prowazek, 1907) from the orang. *P. brasilianum* (fig. 15) recorded by Gonder and Gossler (1908) from a Brazilian monkey, *Brachyurus calvus*, resembles *P. malariae*, the parasite of quartan malaria in man, and *P. reichenowi* (fig. 19) (Sluiter, Swellengrebel, and Ihle, 1922) is said to be similar to *P. falciparum* of human estivo-autumnal malaria.

Reichenow (1917, 1920b) has described parasites in chimpanzees and gorillas in the Cameroons that correspond in their various stages to all three of the species that live in man; he believes the organisms of these anthropoid apes to be the same as the human parasites. Similar results were obtained by Blacklock and Adler (1922) from studies of chimpanzees in West Africa. Adler (1923) found parasites resembling *P. falciparum* in 2 of 13 chimpanzees in Sierra Leone. According to Reichenow (1920b) young animals are more highly parasitized than adults, a fact that is true also in human malaria. Malarial infections in monkeys may be acute or chronic as in man. Quinine appears to be effective against *P. kochi* (Gonder and Rodenwaldt, 1910) and *P. inui* (Leger and Bouilliez, 1913). Attempts to infect mosquitoes by feeding them on malarious monkeys have been mostly negative; Blacklock and Adler (1922) failed to infect *Anopheles costalis* on a chimpanzee and Mayer (1908) likewise failed to infect *Culex pipiens* and *Aëdes argenteus* on monkey blood containing *P. inui*, but he observed what he believes were oöcysts in *Anopheles maculipennis*.

Cross-infection experiments indicate that host-parasite specificity among the malarial organisms of monkeys and man is rather rigid. Halberstädter and Prowazek (1907) were able to transfer *P. pitheci* from orang to orang but not to lower monkeys, and *P. inui* from one *Macacus* monkey to another but not to orangs. Mayer (1908) reports successful inoculations of *P. cynomolgi* into *Macacus cynomolgus*, *M. rhesus* and a *Cercopithecus* monkey. Leger and Bouilliez (1912) were able to infect four species of *Macacus*, three species of *Cercopithecus*, and *Papio anabis* with *P. inui*, but failed to infect *C. fuliginosus* and two chimpanzees. Efforts to infect man with blood from monkeys have not succeeded; Gonder and Rodenwaldt (1910) attempted to parasitize two human beings with *P. kochi*, and Blacklock and Adler (1922) failed to infect man by subcutaneous and intravenous injections of malarious blood from chimpanzees. Mesnil and Roubaud (1917, 1920) claim to have infected a chimpanzee with human blood containing *P. vivax*, but attempts by other investigators to transfer infections from man to monkeys have failed (for example, Blacklock and Adler, 1924).

BABESIA OF MONKEYS

So far as is known to the writer there are no representatives of the genus *Babesia* that live in man. Babesias, or piroplasmas, occur especially in cattle, horses, sheep, goats, and dogs, where they may give rise to destructive diseases such as Texas fever in cattle and haemoglobinuric fever in horses. Several apparently authentic cases of *Babesia* in monkeys are on record. Ross (1905) discovered organisms belonging to this genus, to which he gave the specific name *pitheci*, in a species

of *Cercopithecus* in Uganda; and Kikuth (1927) reports the occurrence of similar organisms, also in a *Cercopithecus* monkey. Symptoms of fever and anaemia appeared, and the blood picture resembled that of pernicious anaemia in man.

DOUBTFUL PROTOZOAN PARASITES OF MONKEYS

Many bodies that have been observed in the blood of monkeys have been placed by investigators in various groups of protozoa. Some of these are probably not protozoa and others not even living organisms. In this category may be included the following. Thézé (1916) describes as a *Toxoplasma* bodies found by him in the blood cells of a monkey, *Mycetes seniculus*, in Guiana; A. Leger (1922) names bodies he observed in the blood cells of a rhesus monkey in Annam, *Grahamella rhesi;* and Langeron (1920) and Leger and Bedier (1922) record as *Haemogregarina cynomolgi* and *H. cynomolgi* var. *papio* bodies seen by them in malarious monkeys (*Macacus cynomolgus* and *Papio sphinx*).

GENERA AND SPECIES OF PROTOZOA OF MONKEYS AND MAN

A comparison of the protozoan parasites of monkeys and man is presented in the following table.

Protozoan Parasites of Man	Protozoan Parasites of Monkeys
Amoebae	**Amoebae**
1. *Endamoeba histolytica*	*Endamoeba nuttalli* (= *E. histolytica*?)
2. *Endamoeba coli*	*Endamoeba pitheci* (= *E. coli*?)
3. *Endamoeba gingivalis*	.....
4. *Endolimax nana*	*Endolimax cynomolgi* (= *E. nana*?)
5. *Iodamoeba williamsi*	*Iodamoeba kueneni* (= *I. williamsi*?)
6. *Dientamoeba fragilis*	.....
Intestinal Flagellates	**Intestinal Flagellates**
7. *Trichomonas vaginalis*	*Trichomonas macacovaginae* (= *T. vaginalis*?)
8. *Trichomonas buccalis*	.....
9. *Trichomonas hominis*	*Trichomonas anthropopitheci* (= *T. hominis*?)
10. *Chilomastix mesnili*	*Chilomastix mesnili* var. *simiae* (= *C. mesnili*?)
11. *Giardia lamblia*	*Giardia* sp. (= *G. lamblia*?)
12. *Embadomonas intestinalis*	*Embadomonas wenyoni* (= *E. intestinalis*?)
13. *Tricercomonas intestinalis*	.....
Intestinal Ciliates	**Intestinal Ciliates**
14. *Balantidium coli*	*Balantidium aragãoi* (= *B. coli*?)
15.	*Troglodytella abrassarti*
16.	*Troglodytella abrassarti acuminata*
17.	*Troglodytella gorillae*
Trypanosomes	**Trypanosomes**
18. *Trypanosoma gambiense*	*Trypanosoma gambiense* (?)
19. *Trypanosoma rhodesiense*	*Trypanosoma rhodesiense* (?)
20. *Trypanosoma cruzi*	*Trypanosoma cruzi* (?)
Leishmanias	**Leishmanias**
21. *Leishmania donovani*	.....
22. *Leishmania tropica*	.....
23. *Leishmania brasilianum*	.....
Malarial Parasites	**Malarial Parasites**
24. *Plasmodium vivax*	*Plasmodium vivax* (?)
25. *Plasmodium malariae*	*Plasmodium malariae* (?)
26. *Plasmodium falciparum*	*Plasmodium falciparum* (?)
Other Protozoa	**Other Protozoa**
27. *Isospora hominis*	.....
28. *Sarcocystis* sp.	.....
29.	*Babesia pitheci*

All of the protozoa usually recognized by protozoologists as human parasites are listed in the above table. Many species described from monkeys have not been included, however, because of their more or less doubtful validity; this applies particularly to amoebae, trypanosomes, and malarial organisms. Further study may prove that certain of these are specifically distinct, but at present our information regarding them is for the most part too scanty to warrant definite decisions.

The table shows that of the four genera of amoebae that live in man, three are represented among monkey amoebae and the fourth has probably not yet been discovered on account of its rarity. Four of the six well-authenticated species of human amoebae are indistinguishable from four species of amoebae that have been described from monkeys. No amoebae in monkeys have been found corresponding to two of the human species, *Endamoeba gingivalis* of the mouth and *Dientamoeba fragilis* of the intestine. Among the intestinal flagellates of monkeys are five species that are indistinguishable from five of the seven species that live in man; *Trichomonas buccalis* of the mouth and *Tricercomonas intestinalis* of the intestine of man appear to be absent in monkeys. The ciliate, *Balantidium coli*, that lives in man is probably the same species that has been recorded from various species of monkeys. Certain monkeys are infected with a genus of ciliates, *Troglodytella*, of which two species and one variety have been described, that has no representatives in man. All three species of human trypanosomes seem to be present as natural parasites of monkeys. The leishmanias have not been reported from monkeys. Malarial parasites that occur in monkeys resemble the three species that live in man. The coccidium, *Isospora hominis*, of the human intestine and the sarcosporidia that have been reported a few times as muscle parasites of man have not been recorded from monkeys. No parasite corresponding to *Babesia pitheci* of monkeys occurs in man. Thus eleven of the fifteen genera of human protozoa are known to have representatives in monkeys; and seventeen of the twenty-five species of human protozoa have been described from monkeys. One genus of ciliates, *Troglodytella*, and one *Babesia* occur in monkeys but not in man.

GENERA AND SPECIES OF PROTOZOA IN LOWER ANIMALS

The significance of this situation can best be realized by comparing the protozoan parasites of man with those of other lower animals. Such a comparison brings out the fact that although many lower animals are inhabited by protozoa belonging to certain of the same genera as those of man the species can be distinguished without difficulty from human protozoa. Thus the rat is infected with species of intestinal amoebae (e.g., *Endamoeba muris*) and intestinal flagellates (e.g., *Giardia muris*, *Trichomonas muris*), and with blood-inhabiting flagellates (*Trypanosoma lewisi*), but not a single species of the rat is considered by protozoologists to be identical with any human species. Certain genera and many species, however, have been described from rats that do not occur in man. Other mammals whose protozoan parasites are fairly well known, such as cats, dogs, guinea-pigs, pigs, sheep, cattle and horses, are similar to rats in this respect. Spontaneous infections in lower animals with human protozoa have been observed, for example, cats and dogs with amoebiasis apparently due to *Endamoeba histolytica*, and rats with giardiasis as a result of ingesting cysts of the human giardia, *G. lamblia*, and in many of them infections with human protozoa can be

set up in the laboratory, but the lower animals are obviously not natural hosts of human protozoa and only become infected with them in nature under extraordinary conditions (Hegner, 1926a). In susceptible lower animals the course of the infection is often very different from that in monkeys and man. For example, the course of amoebiasis in man usually includes a rather long incubation period, followed by acute dysentery from which the patient recovers in a carrier condition, i.e., the infection continues but is kept down by the resistance of the body below the point at which symptoms appear. Active amoebae only are present during the dysenteric period and chiefly cysts are passed during the carrier period; whereas in cats the incubation period is short, death usually occurs as the result of acute dysentery, and no cysts are formed at any time. In monkeys amoebic dysentery runs a course similar to that in man.

PROTOZOAN PARASITES AND THE GENETIC RELATIONSHIP OF HOSTS

Parasites have been used to a slight extent in the study of the genetic relationships of hosts. Von Jhering in 1902 was among the first to discuss this problem in cases of parasitic worms. He argues that two species of hosts are of common descent if they are parasitized by the same species or nearly related species of parasites. He believes that the close relationship of the parasites indicates that they come from a common ancestor and that the different species of hosts involved descended from an ancestral host that was infected by the ancestral parasite. The most important work of this type involving protozoa is that of Metcalf (1923) on frogs and their ciliate parasites of the family Opalinidae. Metcalf discusses, for example, the distribution of the family Leptodactylidae. These are "frogs" characteristic of two widely separated geographical regions, (1) tropical and semi-tropical America and (2) Australia and Tasmania; they have been reported from no other parts of the world. There are two hypotheses that may account for this discontinuous distribution: (1) there may have been a former connection between Patagonia and Australia by way of Antarctica over which these frogs were continuously distributed, or (2) resemblances of the frogs of America and Australia may be due to convergent or parallel evolution.

Frogs of the family Leptodactylidae contain, in the rectum, opalinid parasites of the genus *Zelleriella*. These parasitic ciliates are present in frogs of this family living in both America and Australia. They are so nearly alike in the frogs of the two regions that they can be separated specifically only with difficulty. It is possible that either the frogs or the opalinid ciliates may have arisen by convergent or parallel evolution. It seems very improbable, however, that both the frogs and opalinids arose in this way. The conclusion is reached that the first hypothesis is correct and that a former land connection existed between Patagonia and Australia by means of which frogs of this family, together with their opalinid parasites, migrated to Australia.

PROTOZOAN PARASITES AND THE GENETIC RELATIONSHIPS OF MONKEYS AND MAN

So far as known to the writer no studies have been made to determine genetic relationships among monkeys with the aid of their parasitic protozoa. In fact, probably not enough is known regarding the protozoa of monkeys to make such a study profitable at present. However, as the data compiled in this paper indicate,

the protozoan parasites of monkeys and man belong for the most part to the same species or are so similar in their structure, life-cycles, and host-parasite relations as to be practically indistinguishable. This situation is particularly striking when the protozoa of monkeys are compared with those of other animals associated with man. If the proposition that close relationships of parasites indicate a common ancestry of their hosts is valid, then the facts available regarding the protozoan parasites of monkeys and man furnish evidence of importance in favor of the hypothesis that monkeys and man are of common descent.

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HALDANE ON SELECTION

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THE modern theories of inheritance are sufficiently definite to tempt the mathematically inclined to subject them to analysis for the sake of determining the consequences that flow from them. Pearson (1), Warren (2), Norton (3), and Jennings (4) have dealt with certain phases of the problem, but by far the most thoroughgoing treatment has been given in a series of papers by J. B. S. Haldane (5). The present article is a review of the method of approach and the results obtained in this excellent series of papers.

The author has defined the general problem by stating that when given (1) the mode of inheritance of the character considered, (2) the system of breeding in the group of organisms studied, (3) the intensity of selection, (4) its incidence (that is, on both sexes or only one), it should be possible to state the value of (5) the rate at which the proportion of organisms showing the character increases or diminishes, in terms of (3) the intensity of selection. Conditions (1), (2), and (4) define the problem as to its position in the general theory of inheritance, and (3) and (5) are the variables whose interrelationship we wish to determine within the universe defined by (1), (2), and (4). To formulate the problem mathematically, the author defines intensity of selection by the statement that "if a generation of zygotes immediately after fertilization consists of two phenotypes A and B in the ratio $pA:1B$, and the proportion which forms a fertile union is $pA:(1-k)B$, we shall describe k as the coefficient of selection". This index k is used by the author to measure the intensity of selection, and it may take values between 1 and $-\infty$. At the extremes selection is complete, for when $k = 1$, no B's reproduce and when $k = -\infty$, no A's reproduce. When k is small, selection is slow; if k is positive, it is in favor of the A's and if negative, in favor of the B's.

If the nth generation consists of types A and B in the ratio u_n $A:1B$ $\left(\text{or if the proportion of } B\text{'s in the total universe is } y_n \text{ where } y_n = \frac{1}{1 + u_n}\right)$, the problem resolves itself into the determination of the functional relationship between u_n (or y_n) and k, under different modes of inheritance and different systems of breeding.

All of the papers of this series are concerned with the determination of such functional relationships under a wide variety of conditions, and the consideration of some of the general conclusions that follow from such an analysis.

The first paper deals with some of the

different cases that arise when selection of small and constant intensity operates on Mendelian populations where generations do not overlap either during random mating or when all zygotes are self-fertilized. The cases considered and their results are as follows:

CASE A: SELECTION IN THE ABSENCE OF AMPHIMIXIS

The simplest form of selection is uncomplicated by amphimixis and is illustrated in the following cases:

1. Organisms which do not reproduce sexually, or are self-fertilizing.

2. Species which do not cross, but compete for the same means of support.

3. Organisms in which mating is always between brother and sister.

4. Organisms which are haploid during part of the life cycle, provided that the selection of the character considered occurs only during the haploid phase.

5. Heterogamous organisms in which the factor determining the character selected occurs in the gametes of one sex only.

Setting up the functional relationship between y_n and k for this type of selection, the author finds that $y_n = \frac{1}{1 + (1-k)^{-n}}$, when the initial conditions are such that the number of A's equals the number of B's. For small values of k, that is, when selection is slow, this formula becomes approximately $y_n = \frac{1}{1 + e^{kn}}$, the logistic reaction. For this condition, we see that the proportion of B's falls slowly for a time, then more rapidly, and then slowly again, the most rapid change in the proportion occurring when the number of B's is equal to the number of A's, that is, when $y_n = \frac{1}{2}$. For this mode of inheritance, selection proceeds more rapidly than for any of the other systems of inheritance considered. The speed must compensate to some extent for the failure to combine advantageous factors by amphimixis.

CASE B: SELECTION OF A SIMPLE MENDELIAN CHARACTER

This is the mode of inheritance that has been subjected to mathematical analysis more often than any other. Pearson (6) and Hardy (7) have shown that in the case of random mating, the number of heterozygotes is equal to four times the product of the numbers of the two homozygous classes. Thus, if $u_nA{:}1a$ be the proportion of the two types of gametes produced in the $(n-1)^{th}$ generation, then in the nth generation the initial proportions of the three classes of zygotes are $u_n^2AA{:}2u_nAa{:}1aa$. The proportion of recessives to the whole population is $y_n = (1 + u_n)^{-2}$. Now, only $1-k$ of the recessives survive to breed, so that the survivors are in the proportion $u_n^2AA{:}2u_nAa{:}(1-k)aa$. This leads to an expression for u_{n+1} in terms of u_n and k as follows: $u_{n+1} = \frac{u_n(1 + u_n)}{1 + u_n - k}$. It can be easily shown that this result follows from random mating. If, now, we know the original proportion of recessives, and we start with a population $u_0^2AA{:}2u_0Aa{:}1aa$, where $u_0 = y_0^{-1/2} - 1$, we can at once obtain u_1 by use of the equation $u_1 = \frac{u_0(1 + u_0)}{1 + u_0 - k}$, and by use of this recurring formula, we can determine u_n and therefore y_n.

If the selection is complete,—that is, if all of the dominants are killed off or prevented from breeding,—the case becomes very simple, and y_n is equal to unity.

If, on the other hand, all the recessives die, k becomes equal to 1 and the above general equation reduces to $y_n = y_0(1 + ny_0^{1/2})^{-2}$. This equation shows that

999 generations would be needed to reduce the proportion to one in one million, and we need not therefore be surprised that recessive sports still occur in most of our domestic breeds of animals.

For the case where selection is not very intense, the author has simplified the general recurring equation to the form $kn = u_n - u_0 + \log_e \frac{u_n}{u_0}$. Then starting from or working toward a standard population containing 25 per cent recessives, for which $u_0 = 1$, we have $kn = u_n + \log_e u_n - 1$. This equation gives to a sufficiently exact degree of approximation the relationship between n the number of generations, k the intensity of selection, and u_n. Since making k negative gives the effect of a selection that favors the recessives at the expense of the dominants, we can use this equation and the equation $y_n = (1 + u_n)^{-2}$ to compute for different values of kn the proportion of recessives when either dominants or recessives are favored. This the author has done in Table I, so that we may use this table to run forward and backward from a standard population of 75 per cent dominants and 25 per cent recessives, and determine the change in the per cent of recessives for any number of generations.

Table 2 has been set up from the same equation except that values of kn are tabulated against the percentages of the favored type. These two tables are very convenient for the solution of various actual examples in selection.

TABLE 1

Effect of slow selection on an autosomal Mendelian character

kn (number of generations × k)...	−1000	−100	−50	−20	−15	−10
Per cent of recessives when dominants are favored.....					99.9998	99.975
Per cent of recessives when recessives are favored.....	0.0001	0.0105	0.0427	0.2773	0.4215	1.036

−9	−8	−7	−6	−5	−4.5	−4	−3.5	−3
99.933	99.82	99.50	98.68	96.50	94.38	91.14	86.36	79.71
1.254	1.545	1.940	2.497	3.308		4.537		6.528
−2.5	−2	−1.5	−1	−0.5	0	0.5	1	1.5
71.24	61.53	50.68	40.98	32.05	25.0	19.53	15.30	12.11
	9.718	12.11	15.30	19.53	25.0	32.05	40.98	50.68
2	2.5	3	3.5	4	4.5	5	6	7
9.718		6.528		4.537		3.308	2.497	1.940
61.53	71.24	79.71	86.36	91.14	94.38	96.50	98.68	99.50
8	9	10	15	20	50	100	1000	
1.545	1.254	1.036	0.4215	0.2773	0.0427	0.0105	0.0001	
99.82	99.933	99.975	99.9998					

CASE C: FAMILIAL SELECTION OF A SIMPLE MENDELIAN CHARACTER

This is a case of a factor A, whose presence gives an embryo possessing it an advantage measured by k over those members of the same family which do not possess it. For this case the law used in the preceding section does not hold.

If the family has both parents in common, as in mammals, and we let the population consist of $p_nAA{:}2q_nAa{:}r_naa$, where $p_n + 2q_n + r_n$ = unity, then in a

mixed family where equality would have been expected, the ratio of dominants to recessives will be $1:1-k$. For the case where k is small, we can let $u_n = \frac{p_n + q_n}{q_n + r_n}$, and arrive at the following relationship: $u_{n+1} = u_n + \frac{ku_n}{2(1 + u_n)}$, which in turn may be simplified to give a relationship between u_n and k as follows: $1/2kn = u_n + \log_e u_n - 1$. A comparison of this last relationship with the one derived for selection of a simple Mendelian character shows that the species changes its composition at one-half the rate at which it would change if selection worked on the species as a whole, and not within families only.

If the family has the mother only in common, but fathers are a random sample of the population, as in the case in cross-pollinating seed plants, we find a relationship of the type $3/4kn = u_n + \log_e u_n - 1$ for the case where k is small. Thus selection proceeds at three-quarters of the rate which exists in the case of a selection of a simple Mendelian character.

CASE D: SEX-LIMITED CHARACTERS AND UNISEXUAL SELECTION

When the characters appear in only one sex, as in the case with milk-yield or other secondary sexual characters, we may let the $n-1$ generation form spermatozoa in the ratio $u_nA:1a$, and eggs in the ratio $v_nA:1a$, in which case the nth generation consists of zygotes in the ratio $u_nv_nAA:(u_n + v_n)\,Aa:1aa$. In this case, $y_n = (1 + u_n)^{-1}(1 + v_n)^{-1}$. With complete selection, when $k = -\infty$, this case reduces to $y_n = 1 + 2^{1-n}(y_0^{1/2} - 1)$, where the proportion of dominants is halved in every successive generation. When $k = 1$, and all the recessives of one sex die childless, the proportion of recessives in successive generations, starting from the standard populations, is 25 per cent, 16.7 per cent, 12.5 per cent, 9.56 per cent, 7.94 per cent, etc. When the rate of selection is slow,—that is, k is small,—our equation becomes $1/2kn = u_n + \log_e u_n - 1$, which shows that selection proceeds at one-half the rate for slow selection of a simple Mendelian character.

TABLE 2

Effect of slow selection on an autosomal Mendelian character

Per cent of favored type					0.0001	0.001	0.01	0.05
kn when dominants are favored					−15.51	−13.21	−10.90	−9.294
kn when recessives are favored					−1005.0	−320.0	−102.60	−45.50
0.1	0.2	0.5	1	2	3	5	10	15
−8.600	−7.905	−6.996	−6.286	−5.580	−5.161	−4.624	−3.863	−3.290
−33.04	−23.42	−14.72	−10.197	−6.875	−4.976	−3.717	−1.933	−1.041
20	25	30	35	40	45	50	55	60
−2.979	−2.712	−2.439	−2.180	−1.964	−1.708	−1.467	−1.220	−0.962
−0.448	0	+0.366	+0.681	+0.962	+1.220	+1.467	+1.708	+1.964
65	70	75	80	85	90	95	97	98
−0.681	−0.366	0	+0.448	+1.041	+1.933	+3.717	+4.976	+6.875
+2.180	+2.439	+2.712	+2.979	+3.290	+3.863	+4.620	+5.161	+5.580
99	99.5	99.8	99.9	99.95	99.99	99.999	99.9999	
+10.197	+14.72	+23.42	+33.04	+45.50	+102.60	+320.0	+1005.0	
+6.286	+6.996	+7.905	+8.600	+9.294	+10.90	+13.21	+15.51	

This result was previously given by Punnett (8).

CASE E: SELECTION OF AN ALTERNATIVELY DOMINANT CHARACTER

Certain factors, such as those determining the presence or absence of horns in Dorset and Suffolk sheep according to Wood (9), are dominant in one sex and recessive in the other. With complete selection, all members of the type dominant in the female sex are weeded out. With $k = 1$, the type disappears in the male sex and is halved in successive female generations. If $k = -\infty$, the recessive type in the female sex disappears in that sex and is halved in successive male generations. For small values of k, that is, for a low rate of selection, we have $kn = 2\log_e u_n$, so that selection occurs on the whole more rapidly than in the case of a simple Mendelian character.

CASE F: BISEXUAL SELECTION OF A SEX-LINKED CHARACTER

The case of selection in a population whose members differ with regard to a sex-linked factor leads to the conclusion that for complete selection, no dominants survive to breed and the selection is complete in one generation. If $k = 1$, and no recessives survive to breed, there are no recessive females produced and the number of recessive males is halved in each generation. Selection is therefore vastly more effective than on an autosomal character. If colorblind or hemophilic people were prevented from breeding, these conditions would be almost abolished in a few generations, which would not be the case with feeble-mindedness.

In the case of slow selection, if generations are reckoned from a standard population when $u_0 = 1$, and 50 per cent of the males and 25 per cent of the females are recessives, we find that within an error of the order of k, we have

$$kn = \log_e u_n + 2 \log \left(\frac{3 + u_n}{4} \right)$$

and

$$y_n = (1 - u_n)^{-2}$$

$$z_n = (1 + u_n)^{-1}$$

when y_n = per cent of recessives of the homozygous sex and z_n = per cent of recessives of the heterozygous sex. Thus selection acts more rapidly on a sex-linked character in the homozygous sex than on an autosomal character and at about the same rate in the heterozygous sex as on an autosomal character.

CASE G: BISEXUAL FAMILY SELECTION OF A SEX-LINKED CHARACTER

Considering the case where the family within which selection occurs has both parents in common and letting the dominants have an advantage of 1 to $1 - k$ over the recessives in the mixed families, the author finds that with complete selection for $k = 1$ the recessives disappear at a very fast rate. When k is small, the selection proceeds more as in the case of racial selection, but at from one-half to one-third of the rate.

CASE H: SELECTION OF A SEX-LINKED CHARACTER IN THE HOMOZYGOUS SEX ONLY

Several sex-linked factors are known which have a much more marked effect on the homozygous than the heterozygous sex; thus in *Drosophila melanogaster* "fused" females are sterile, males are fertile, while the character "dot" occurs in 8 per cent of the genetically recessive females, but only 0.8 per cent of the males (Morgan and Bridges, 10). Under these conditions, with complete selection for $k = -\infty$, the dominants disappear in two generations.

If $k = 1$, the elimination is vastly slower than when selection occurs in both sexes. If k is small, the selection of the homozygotes proceeds as in the case of slow selection on an autosomal Mendelian character, while the heterozygous sex changes rather more slowly.

CASE I: SELECTION OF A SEX-LINKED CHARACTER IN THE HETEROZYGOUS SEX ONLY

In certain cases, sex-linked factors appear only or mainly in the heterozygous sex. For example, in *Drosophila melanogaster* "eosin" eye-color is far more marked in the male than in the female, and the sex-linked fertility factor L_2 postulated by Pearl (11) in poultry can show only in the female sex. Under these conditions we find that for complete selection, $k = -\infty$, the number of dominants is halved in each generation after the second. If the recessives are eliminated and $k = 1$, the proportion of recessives is halved in each generation. If the selection is slow, $kn = 3 \log u_n$ and the selection of the heterozygous sex proceeds along the logistic curve but at one-third the rate of an autosomal Mendelian character, while the selection in the homozygous sex is slightly faster.

CASE J: CERTATION, OR GAMETIC SELECTION OF AN AUTOSOMAL CHARACTER

Gametes or gametophytes may be selected according to what factors they carry, and while such selection may be wide, it is more likely to be among the gametes of the same individual. Considering the gametes of one gender to be affected by selection, we find that for complete selection if all the dominant-carrying gametes are eliminated, $k = -\infty$, the proportion of dominants is halved in each generation. If all recessive carriers are eliminated, no recessive zygotes appear and the proportion of heterozygotes is halved in each generation. If selection is slow,

$$kn = 2 \log_e u_n$$

and

$$y_n = (1 + u_n)^{-2}$$

A comparison of the results of complete selection for the more important cases is given in Table 3. Selection is supposed to begin on a population in equilibrium, containing equal numbers of dominants and recessives of the sex considered. The author comments on this table as follows: "It is worth noting that in the case of sex-linked characters, and autosomal recessives when selection is gametic, individuals of types which have wholly disappeared reappear if selection ceases. With many types of heredity dominants are eliminated in one or two generations, and where this is not the case they generally decrease more rapidly than recessives."

The rate of slow selection has been determined less rigorously than in the case of rapid selection, but the effect of the approximation is slight. Table 4 shows the effect of slow selection in the various cases considered, the rate of selection in this case being one in a thousand, that is, a thousand of the type considered survive for every 999 of the other.

A consideration of all of the cases dealt with in this paper shows that selection is most rapid when amphimixis is avoided by one means or another. Moreover, selection is ineffective on recessive characters when these are rare, except in the case of sex-linked factors, when it is effective in the homozygous sex and in gametic selection. It seems, therefore, very doubtful whether natural selection in random mating organisms can cause the spread of autosomal recessive

characters unless they are extraordinarily valuable to their possessors. Such characters appear far more frequently than dominant mutations, but in their early states are selected infinitely more slowly.

In Part II (5) of this series of papers, the author considers the influence of partial self-fertilization, inbreeding, assortative mating, and selective fertilization on the composition of Mendelian populations and on natural selection, and finds that for partial self-fertilization and partial inbreeding, the selection is rapid when the recessives are few. Partial assortative mating and selective fertilization on the other hand have but slight effect on the rapidity of selection. The case of inbreeding is of importance since the moderate degree of inbreeding which must occur in human populations in such instances as the mating of cousins will enormously increase the number of recessives when these recessives are sufficiently rare. Assortative mating, which has been shown by Pearson (12) to exist in human populations, will on the other hand have but little effect. Hence, inbreeding or self-fertilization appears to be necessary in early stages of selection of a recessive character if this process is to be fast enough to be an effective cause of evolution. Inbreeding and self-fertilization cannot be replaced by moderate degrees of selective mating or fertilization.

TABLE 3

Effects of complete selection

CHARACTER ELIMINATED	TYPE OF SELECTION	SEX	PER CENT AFTER 5 GENERATIONS FROM 50 PER CENT	PER CENT AFTER 10 GENERATIONS FROM 50 PER CENT
Non-amphimictic	Any	Both	0	0
Autosomal dominant	Bisexual	Both	0	0
Autosomal recessive	Bisexual	Both	2.44	0.768
Autosomal dominant	Unisexual	Both	1.83	0.0572
Autosomal recessive	Unisexual	Both	8.88	3.27
Sex-linked dominant	Bisexual	Homozygous	0	0
		Heterozygous	0	0
Sex-linked recessive	Bisexual	Homozygous	0	0
		Heterozygous	1.56	0.0484
Sex-linked dominant	In homozygous sex	Homozygous	0	0
		Heterozygous	0	0
Sex-linked recessive	In homozygous sex	Homozygous	5.34	1.74
		Heterozygous	18.5	13.28
Sex-linked dominant	In heterozygous sex	Homozygous	1.83	0.0572
		Heterozygous	3.125	0.0977
Sex-linked recessive	In heterozygous sex	Homozygous	0	0
		Heterozygous	3.125	0.0977
Autosomal dominant	Gametic unisexual	Both	1.83	0.0572
Autosomal recessive	Gametic unisexual	Both	0	0

In Part III (5), the author considers the cases of a single but completely dominant factor and of several interacting factors. Mating is supposed to be at random, the populations to be very large, and the generations not to overlap. He derives for these cases expressions for the changes caused by slow selection in

populations whose characters are determined by incompletely dominant, multiple or polyploid factors, and for the equilibria attained in certain of the cases. For a multiple autosomal recessive character, selection is shown to be lower than in the case of a character determined by one factor alone, although when the dominants are very rare or when one of the multiple factors greatly outweighs the rest, it proceeds at about the same rate in the two cases. Selection is slowest for the multiple case when the factors are of equal weight. Similar results are obtained in the cases of multiple sex-linked recessive characters and multiple autosomal dominant characters, selection being slower in the multiple case.

For the case of linkage between the autosomal factors, the proportions of the various types of gametes are shown to approach asymptotically those which would be reached in one generation without linkage.

Part IV (5) deals with the question of overlapping generations, and in it the author first takes up and demonstrates the theorem previously given by Lotka (13)

TABLE 4

Generations required for a given change with various types of slow selection

$k = 0.001$

DOMINANT FACTOR FAVORED	TYPE OF SELECTION	SEX	CHANGE IN PERCENTAGE			
			0.001–1	1–50	50–99	99–99.999
Non-amphimictic	Bisexual racial	Both	6,921	4,592	4,592	6,921
Autosomal	Bisexual racial	Both	6,920	4,819	11,664	309,780
Autosomal	Unisexual racial / Bisexual familial	Both	13,841	9,638	23,328	619,560
Autosomal	Bisexual familial†	Both	9,227	6,425	15,522	413,040
Autosomal*	Bisexual racial	♂	13,831	8,819	6,157	7,112
Sex-linked	Bisexual racial	Homozygous	6,916	4,668	5,593	10,106
		Heterozygous	6,928	5,164	11,070	20,693
Sex-linked	Bisexual familial	Homozygous	20,753	13,785	13,785	20,753
		Heterozygous	20,768	14,987	24,332	41,450
Sex-linked	Racial of homozygous sex	Homozygous	10,380	7,228	17,496	464,670
		Heterozygous	10,392	8,378	153,893	149,860,377
Sex-linked	Racial of heterozygous sex	Homozygous	20,746	13,228	9,236	10,668
		Heterozygous	20,753	13,785	13,785	20,753
Autosomal	Unisexual gametic	Both	13,831	8,819	6,157	7,112
Autosomal	Unisexual gametic‡	Both	27,661	17,638	12,314	14,224
Sex-linked	Gametic of homozygous sex	Homozygous	10,373	6,619	4,618	5,334
		Heterozygous	10,377	6,892	6,892	10,377
Sex-linked	Gametic of homozygous sex‡	Homozygous	20,746	13,228	9,236	10,668
		Heterozygous	20,753	13,785	13,785	20,753

* Dominant in ♂, recessive in ♀.

† The families have only one parent in common.

‡ In heterozygous individuals gametes are replaced (as zygotes in familial selection).

The effect of selection on recessive characters may be found by inverting the order of the four numerical columns. Thus 309,780 generations are needed for an autosomal recessive to increase from 0.001 per cent to 1 per cent, 11,664 generations to increase from 1 per cent to 50 per cent, and so on.

as to the stability of normal age distribution. Consideration of the effect of generations that overlap to the extent that they do in mankind shows that the changes due to slow selection are very similar to those which occur when generations are separate.

The last paper of the series, Part V (5), considers the subject of mutation. The frequency of occurrence of mutations is generally small, and on the whole, mutants recessive to the normal type occur more commonly than dominants. A consideration of selection in this case shows that if it acts against mutation it is ineffective, provided that the rate of mutation is greater than the coefficient of selection. Moreover, mutation is quite effective where selection is not: namely, in causing an increase of recessives where these are rare. It is also more effective than selection in weeding out rare recessives, provided it is not balanced by back-mutation of dominants. Mutation, therefore, determines the course of evolution as regards factors of negligible advantage or disadvantage to the species, but it can lead to results of importance only when its frequency becomes large.

This series of papers is not only valuable for the large number of cases treated, but it is extremely fertile in suggestions for possible extensions of the analysis. As it stands, it constitutes the most complete mathematical treatment of the effect of natural and artificial selection which has appeared.

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SEASONAL MODIFICATIONS IN TESTES OF VERTEBRATES

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THERE is an obvious relationship between the phenomena of sexual urge and of testicular activity. That the testis augments the mating instinct has long been known, and the literature contains a great deal of controversy concerning which of the testicular elements wields this influence.

In most animals there are seasonal variations in the size of the testis and in the relative quantity of its constituent elements. These changes are found in all animals that mate but once each year. In hibernating animals the changes appear to be more pronounced than in the non-hibernating forms. Where the seasonal changes in sexual behavior and in testicular structure are marked it is reasonable to expect that any parallelism between testicular modification and physiological action might be seen. Such a parallelism might be found between sex activity and (1) volume of a particular tissue or (2) cell proliferation or (3) cytological appearance. Each of these parallelisms has been reported as existing.

It has been difficult to ascertain the importance of any change in any of the tissue substances of the testis, partly because of the scarcity of studied material. This is true because most of the reports found in the literature are based upon observations covering only a few months of the year. A second difficulty has been due to the fact that in many reports the exact time of mating has not been noted. The failure to take into consideration the exact time of breeding rather than the approximate time of the year has caused much of the confusion and difference of opinions. Perhaps the greatest difficulty in studying the physiology of the testis has been caused by the fact that some writers have attempted to prove a theory with their facts instead of forming a theory to explain the observed facts. As a result, the literature contains many contradictory statements that are difficult to interpret.

In this review an attempt has been made to glean the facts from the literature upon seasonal changes in vertebrate testes and to present these facts in as clear a manner as possible. In order to do this the literature on the seasonal changes in each group of animals is reviewed separately and an attempt is made to evaluate these observations. The recorded observations are then discussed and interpreted with reference to the known facts regarding the time and peculiarities of sexual activities of these animals.

MODIFICATIONS IN THE TESTES OF FISH

Fish testes are made up of lobules containing cysts of germ cells. These lobules correspond to the spermatogenic tubules of mammals and empty into longitudinal collecting ducts which in turn open into

the epididymis and vas deferens. During the non-spermatogenic season these lobules are small and contain only a few germ cells. All cells in any one lobule are of one stage of development, the testis in this respect resembling that of arthropoda. As spermatogenesis progresses these lobules become filled with germ cells, and as the number and size of the cells increase the lobules become enlarged. This continues during multiplication and growth of spermatogonia and spermatocytes and perhaps during the early part of the spermatid period. Thereafter the size of the individual cells decreases without any augmentation in their number and the lobules thereupon decrease in size proportionately. When the sperm are ejected the lobules are emptied and suddenly decrease in volume.

Between the lobules are found connective tissue, blood and lymph vessels, and nerves. When the lobules are distended with spermatogenic tissue they press tightly against each other. The cells of the connective tissue lying between them then resemble typical connective tissue cells. When the lobules decrease in volume, during the spermatid and spermatozoa stages and especially when the spermatozoa are ejected, some of the connective tissue cells enlarge and become somewhat modified in structure. These cells are commonly referred to as interstitial cells and some authors maintain that they are glandular cells.

The entire mass of tissue between the lobules in fishes and amphibia and the tissue between the tubules in birds and mammals should be designated *intertubular tissue*, while the term *interstitial tissue* should include only the modified connective tissue cells. This distinction is necessary since an increase in the space between the tubules, *intertubular space*, does not always imply an increase in interstitial tissue. In a review of the literature this distinction is difficult to maintain since most writers have failed to note the differences, but the fact should not be overlooked in evaluating the reports.

Size of the testis in fish largely depends upon the size of the lobules. When the lobules enlarge the testis increases in volume. When the lobules shrink following sperm ejection the testicular volume does not proportionately decrease because of change in intertubular tissue, especially because of the interstitial cell increase in the case of fishes. Later, as the interstitial cells decrease in quantity, the testis further shrinks in volume.

Temperature of the water, abundance of food, and to some extent the amount of light are prime factors in the life of the fish. Anatomic and physiological seasonal modifications are especially influenced by changes in temperature. For example, if a female about to deposit her eggs is placed in very cold water, egg deposition may be delayed indefinitely.

In Yellow Perch (*Perca flavesans*) Turner (36) reports that the volume of the testis is greatest during late November. He also states that the maximum size is in January. His data indicate that the greatest weight is in November. The volume increase at this time is very rapid because of the increase in the number of germ cells in the lobules. The large size of the testis persists until early March and then suddenly falls when spawning takes place due to ejection of ripe sperm. This decrease continues from early March to late May. The beginning of increase in volume precedes the decline in temperature and is due to the early stages of spermatogenesis. The first spermatozoa are formed in the early part of September and are present in the lobules until their expulsion takes place the following spring. No data were given concerning the intertubular tissue.

Seasonal variations in the size of the

testis of the Top Minnow (*Gambusia affinis*) may be eightfold (18). The period of maximum size is from November to February. No spermatogenesis occurs during cold weather. Again no mention is made regarding interstitial cells. This should not be construed as indicating that they do not exist. The data offered by these two investigators show the relation between testicular size and spermatogenesis. This is in turn directly related to sex activity.

Courrier (12 and 13) reported that in the Stickleback (*Gasterosteus aculeatus*) spermatogenesis occurs during March. It progresses rapidly, so that by the end of the month it is completed and most of the lobules contain spermatozoa.

During spermatogenesis the seminal elements distend the cysts so that they press tightly against each other. Only a thin layer of connective tissue in addition to the blood vessels and nerves then separates the lobules. Courrier records that early in April after the end of spermatogenesis the interlobular spaces begin to change and that in May and June the cells in these spaces are filled with many mitochondria and secretion granules. He refers to these cells as forming an interstitial gland and suggests that they have increased because there exists a need for a product they secrete. According to Courrier, the purpose of these "glandular" cells is to secrete a testicular hormone which produces the bright, nuptial coloration and sex activity. He further states that in May and June fish that do not have the nuptial appearance have no trace of interstitial cells though they have spermatocytes and spermatogonia. These are probably males that mated early and have lost their mating apparel.

Champy (10) found many Sticklebacks with nuptial apparel in the winter but with interstitial cells poorly developed or absent. They are rare or absent at the time that spermatozoa ripen, which is at the opening of the mating season. He studied development in many other species of fish and could find no correlation between presence of interstitial cells and development of secondary sex characters or modifications of appearance that are found during the mating season. In *Spinachia vulgaris*, *Tinca vulgaris*, and *Phoxinus laevis* he found no trace of interstitial cells at any period of the year, yet males of these species develop sex characteristics and mating apparel. He found that these anatomic changes appeared to be correlated with the maturity of spermatozoa.

Van Oordt (37 and 38) also made observations upon *Gasterosteus aculeatus*. He found that the testicle at mating, the exact time of which he fails to designate, contains no spermatocytes but that it is then filled with spermatozoa. Large groups of interstitial cells are then found at the corners of two or three canals. In August, when secondary sex characters are largely gone and the tubules contain early stages of spermatogenesis, the intertubular spaces are quite wide and contain groups of interstitial cells. In October spermatogenesis has continued, distending the lobules, and only a few interstitial cells are then present (38). In winter, when secondary sex characters are not developed, he found some testes in which there existed a broad interstitium with many interstitial cells. In spring he found that secondary sex characters appear as spermatogenesis advances. He concludes from cytological findings that the interstitial cells increase when spermatogenesis is suspended because they become charged with nourishment. This stored up food is later consumed by developing germinal epithelium during the period of cell proliferation.

From the above data it is almost impossible to arrive at any positive conclusions regarding cytological changes throughout the year. Though Courrier, Champy, and Van Oordt made observations on the same species, *Gasterosteus aculeatus*, the data offered are very meager and do not cover the entire year. Much interpolation is necessary. Chart I, which is based on all available data, makes it quite certain that the interstitial cells do not promote the appearance of nuptial apparel in this species. These cells develop after maturity of spermatozoa. They increase as the mating season closes and are most abundant during the summer months, when the testes contain no sperm. When spermatogenesis again takes place they decrease. They follow rather than precede mating and are abundant in the testis when the tubules are empty. The latter fact has been emphasized by Van Oordt, who concludes from this relationship and from the cytological changes taking place in the interstitial cells that they are trophic cells. He maintains that they are abundant when the fatty material they contain is not being consumed by developing germinal cells.

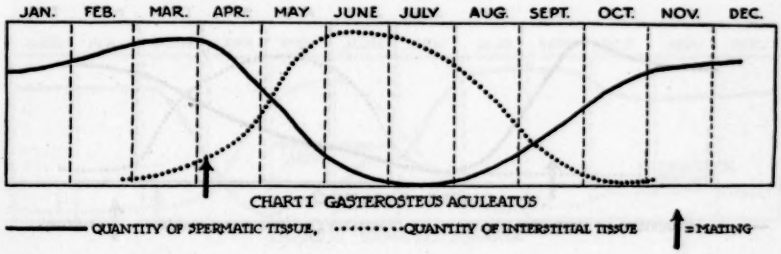


CHART I GASTEROSTEUS ACULEATUS

MODIFICATIONS IN TESTES OF AMPHIBIA

The structure of the amphibian testis somewhat resembles that of the fishes. The spermatogenic cells are found in cysts and lobules, the latter being separated by intertubular tissue. Under certain conditions some of the intertubular connective tissue cells become modified into interstitial cells.

Anura generally breed in the spring, and their eggs may be seen in ponds or along the stream banks during high water of early spring. Urodeles, however, breed largely during midsummer and early fall. Some *may* breed in spring. With each species care must therefore be taken to note the cytological modifications of the testis and the anatomic and physiologic peculiarities with reference to the actual time of mating rather than to calendar month or seasonal period of the year. In most species spermatogenesis takes place in the summer immediately after mating and the spermatozoa are retained in the testis and spermatic passages during the winter.

Friedman (15) found tubuli of *Rana fusca*—now *Pelobates fuscus*—well filled with spermatogonia at the end of March, through April and May, and even in June. The tubules are angular in outline at that time from being pressed tightly together. There is little room for intertubular substance, and only blood vessels and connective tissue cells are present between the tubules. Toward the end of June, with spermatogenic progress, interstitial cells appear. In the fall, when all stages of spermatogenesis are found, the intertubular spaces are richly filled with interstitial

cells. At the end of October and during the winter months, when no spermatogenesis is going on (only spermatogonia are found), the interstitial cells disappear.

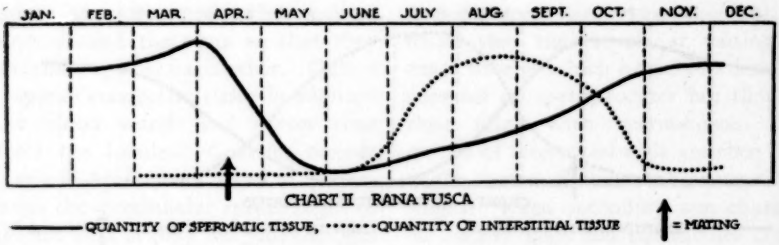
He does not indicate when mating occurs, merely stating that spermatogenesis is going on during the summer and that at the end of October only spermatogonia are present. From this it might be inferred that mating is in October when the products of the summer and fall wave disappear. From other sources of information it seems that the mating period is from the middle of March to the middle of May. Friedman was apparently observing the early stages of a wave of spermatogenesis whose products are kept until the following spring, as is true for other Amphibia.

Nor does he record the size of the tubules during spermatogenesis, though from his discussion of the early spring and late fall and winter conditions it appears that from June to September the tubules are not distended but round and the intertubular space is large.

Mazzetti (27) confirmed Friedman's report for *Rana fusca*. He stated that in the fall, when all stages of spermatogenesis are found, there is an abundance of interstitial tissue. Toward the end of October spermatogenesis ceases and the interstitial cells diminish little by little until they are no longer demonstrable. He does not state, as does Friedman, that spermatozoa are not present at this time, but only reports that no spermatogenesis is taking place.

Chart II is based upon Friedman's report of *Rana fusca* together with information supplied by Mazzetti. It shows very well that the increase in size of the testis with spermatogenesis is accompanied by interstitial cell decrease. It also clearly indicates that the interstitial cell increase follows mating and does not precede it.

In *Rana viridis*, now known as *Rana esculenta*, Friedman observed all stages of spermatogenesis during late summer and fall. From June to October most of the tubules are small. After this spermatogenesis takes place. During early August the interstitial cells are well developed. In winter, when spermatogenesis continues and the tubules are distended, interstitial cells are no longer present. Mazzetti also made observations on the testes of this frog and reports that the interstitial cells are abundant during the period of intense spermatogenesis (time not given, nor are his criteria for intense spermatogenesis stated). His work is not thorough and is confined to the fall season.



Champy (7) observed that in *Rana esculenta* during July the interstitial cells undergo a regressive change and take on the aspect of connective tissue cells. Spermatogenesis is then most active. In autumn, when spermatogenesis is arrested,

the interstitial cells little by little become granular and increase both in number and in volume. This increase continues until January, when fat granules fill the cytoplasm of the interstitial cells. He traces the fat from these cells into the tubules during the following months. Mating takes place in April and May, and at this time the interstitial cells are at their minimum. After mating the interstitial cells rapidly increase. The tubules are empty in June. Spermatogenesis proceeds rapidly during the first part of July, and with equal abruptness the interstitial cells, deprived of their fat, return to fibroblasts. *Rana esculenta* resembles *Rana fusca*. The differences are matters of detail only.

interstitial cells increase after the mating season when the tubules have been emptied of sperm. Chart III from Champy's data on *Rana temporaria* shows that interstitial cell increase follows mating and accompanies ejection of spermatozoa from the lobules.

Friedman found that in the tree frog (*Hyla arborea*) the tubules are full of dividing cells throughout the month of July and the intertubular space is then very small. It contains only a few interstitial cells here and there among the connective tissue cells. In September, when spermatozoa are formed, the interstitial tissue is very rich and contains much fat. In October most of the tubules contain only spermatozoa, the quantity of intertubular

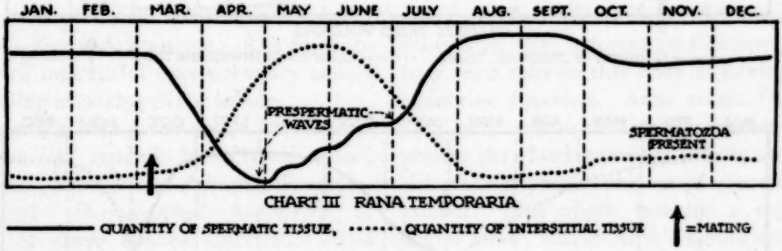


CHART III RANA TEMPORARIA

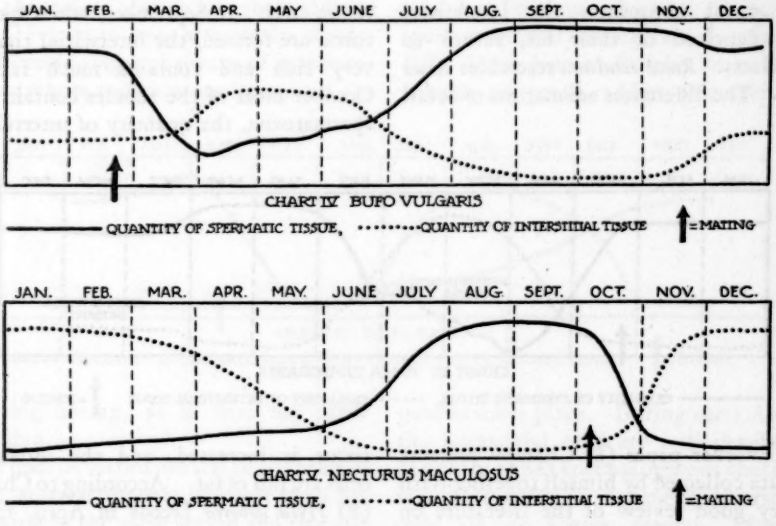
——— QUANTITY OF SPERMATIC TISSUE, ····· QUANTITY OF INTERSTITIAL TISSUE ↑ =MATING

In another paper (8) Champy presents all data collected by himself together with a very good review of the literature on Amphibia. His charts show the quantity of interstitial cells, but they do not give an exact picture of the quantity of spermatogenic tissue. In *Rana esculenta* for example, there is no spermatogenic tissue present immediately before or during mating. This is because Champy has presented intensity of spermatogenic activity and not quantity of germinal tissue. He states (8, p. 25) that in *Rana temporaria* the variation is still more marked than in *Rana esculenta* because only one wave of spermatogenesis takes place each year. Here again the fact is made clear that the tissue is increased, and the interstitial cells are full of fat. According to Champy (8) *Hyla arborea* breeds in April, not in September or October. Friedman was apparently observing fall spermatogenesis, common to Anura, and in some way became confused regarding the mating season. Friedman also reported that in the toad (*Bufo vulgaris*) the interstitial tissue reaches its greatest development during spermatogenesis. These findings were confirmed by Mazzetti (27) in a general paper almost completely lacking in data. But Champy's (8) careful study shows that these authors apparently erred in their reports. He states (p. 262) that the testicular changes in *Bufo vulgaris*

resemble those of other Anura, and a chart built from his observations is herewith presented. See Chart IV.

Champy also reports that interstitial tissue is abundant during winter in *Rana esculenta*, *Hyla arborea*, *Bufo calamita*, *B. vulgaris*, *B. pantherina*, and *Alytes obstetricans*. Similarly he found that prespermatogenesis takes place throughout the year in each of these frogs and toads except *Alytes*.

Urodeles are much like anurans in the interstitial gland, but he adds that it is difficult to admit that the interstitial tissue is endocrine in function (8, p. 266) because he was unable to find the supposed relation between the development of secondary sex characters and the development of the interstitial tissue (p. 270). He therefore believes that in those anurans having prespermatogenesis the hormone is produced by this abortive spermatogenesis. Champy looks upon prespermatogenesis, especially in urodeles, as a process


JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SEPT. OCT. NOV. DEC.
CHART IV BUFO VULGARIS
QUANTITY OF SPERMATIC TISSUE, QUANTITY OF INTERSTITIAL TISSUE
=MATING
JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SEPT. OCT. NOV. DEC.
CHART V. NECTURUS MACULOSUS
QUANTITY OF SPERMATIC TISSUE, QUANTITY OF INTERSTITIAL TISSUE
=MATING

respect to testicular modifications. Champy emphasizes this similarity, and Chart V of *Necturus maculosus*, constructed from Humphrey's data, shows that this is true. Champy noted that in *Salamandra maculosa*, *S. atra*, and *Amblystoma tigrinum* interstitial cells appear after the spermatozoa are expelled. When spermatogenesis takes place they degenerate.

Champy places emphasis upon prespermatogenesis, found in both anurans and urodeles. He states that in anurans this endocrine function is performed by of forming a "*corpus jaune testiculaire*," which produces the hormone. He states (8), however, that these bodies develop after the appearance of the secondary sex characters.

Humphrey (21, 22, and 23) has made a very complete study of the interstitial cells in urodeles. He reports that in *Necturus maculosus* few or no spermatozoa are present in the testis during the winter. These entirely disappear from the testis before the end of the following April. Spermatogonial division may be seen dur-

ing the winter. In the spring and early summer division and growth of germ cells take place. By October spermatozoa are mature, and at the end of that month the greater portion of the testis is again empty. The testis during July, August, and September is at the greatest size it attains at any time. The lobules are then enlarged and angular rather than circular, with blood vessels occupying the spaces where three or more tubules meet. No cells recognizable as interstitial cells can be found at this time. In late October the interstitial cells are developed from stromal cells, a process beginning in the caudal portion of the testis following departure of mature spermatozoa. According to Humphrey their development is to be looked upon as correlated with the regressive phase of spermatogenesis and not as a seasonal condition. The development of interstitial cells normally occurs following emptying of the lobule.

What has been given above for *Necturus* is true in general for *Cryptobranchus*, *Plethodon*, *Diemyctylus*, *Splerepes*, *Gyrinophilus*, and *Desmognathus*. Moreover, in some of these species interstitial cells completely disappear while, and even before, spermatogenesis proceeds.

Chart V, built from data offered in Humphrey's papers, shows clearly, as stated by that author, that interstitial cell development follows degeneration within the lobule and that it is not a seasonal condition. He offers much data clearly analyzed in support of his conclusions. This chart shows that the breeding season must be carefully noted, for in this species the interstitial cells are abundant during spring, when most species breed, but are at a minimum during October, its true breeding season. In a recent communication Humphrey states that he "is not sure that the breeding period has been clearly established. Animals have sperm in their vasa deferentia for some time after the testis empties. Necturus males are *capable of mating* in spring as well as in the fall. This is also true of *Plethodon*, *Diemyctylus*, *Spelerpes*, and other urodeles. The mating season may extend over several months."

Aron (3, p. 25) stated that of the divers elements of the testis only the glandular tissue parallels the seasonal evolution of sex characters. This glandular tissue develops by multiplication of Sertoli cells within a cyst (lobule of other authors). The connective tissue cells of the cyst wall also increase. The cyst gradually comes to appear like a corpus luteum. Its walls soon disappear, the cells rapidly atrophy, and a cicatricial tissue with globules of fat is substituted. The formation of this gland as observed by Aron differs somewhat from that reported by Champy, but they both refer to this body as having an endocrine function. Aron states (3, p. 116) that when the sex characters are present the gland is present and that when the gland is present the sex characters are present. This might well be a coincidental affair, but in Aron's hands experimental evidence appears to give it some significance. When he has cauterized this tissue without injury to the remainder of the testis the secondary sexual characters disappear. When the remainder of the testis is removed without injury to this organ the secondary sex characters pursue the normal course. However, the evidence is not conclusive because (1) it is almost impossible to cauterize this portion of the testis without injuring the blood supply to the remainder of the testis and (2) the change resulting from cauterization of this tissue is only a slight speeding up of the disappearance of characters that are soon to disappear as a normal process. Humphrey has also called my attention to the fact that in cauterizing this tissue the

operator is essentially destroying all the germinal tissue and that only empty lobules remain. It is further weakened by the fact that the appearance of secondary sex characters in urodeles just approaching sexual maturity must await the evacuation of the cysts following one spermatogenic cycle, for according to Aron (3, p. 112) only the evacuation of the cysts will introduce the genesis of this endocrine mass.

Humphrey shows that Aron's abortive spermatogenesis and Champy's prespermatogenesis vary in quantity. They are present only in certain species and not always in these. He draws attention to the fact that in testes of urodeles, as of other vertebrates, unfavorable environment causes injury to the germ cells and their degeneration follows. From data presented (Humphrey, 23) the conclusion that this germ cell degeneration is the result of unfavorable conditions in winter seems justified. This does not end in the formation of a true anatomical organ, and there is no need to ascribe a definite function to the degenerating lobules or associated interstitial cells. From this alone it cannot be said that the tissue does not perform a function. But if an endocrine function be ascribed to this tissue it can apply to only a limited number of species, and in these during part of the year. Its limited occurrence makes it seem very improbable that such tissue has an endocrine function in any species.

MODIFICATIONS IN TESTES OF BIRDS

In birds the testicular structure resembles very much that found in mammals. The germinal tissue is found in seminiferous tubules, where waves of spermatogenesis may be seen. The intertubular tissue is composed of lymph and blood vessels, nerves, connective tissue, and some interstitial cells.

Many early investigators reported volumetric and weight changes in birds during the year. Gadow (16) refers to the familiar fact that the testis of the house sparrow enlarges from the size of a seed during winter to that of a cherry during the mating season, at which time it displaces the digestive organs. Disselhorst (14) discusses the increase in volume of the testis approaching the time of mating. In *Fringilla* there is an increase in weight of about three hundred fold. He also cites Leuchhart as finding an increase in weight of one hundred and ninety fold in the Starling from winter to spring. In these reports, cytological data is lacking and only macroscopic information is given.

Stieve (32) reports that in the European Jackdaw (*Colaeus monedula collaris*) there is a fluctuation of four hundred and eighteen volumes in the testis during the year. This volumetric fluctuation is produced by changes in quantity of germinal tissue. In spring the testes increase in size up to April. At this time the tubules are greatly distended with germ cells, and it is then that mating takes place. Thereafter the testes decrease in volume until they reach a minimum size in January. The intertubular tissue is most abundant when the germ cells are at a minimum during winter. It is most abundant during the non-sexual period and least abundant at the time of mating. He refers to the increase in intertubular tissue as an interstitial cell hypertrophy. He is sure that the interstititial cells do not produce the testicular hormone because they are at their minimum when sex activity is at its maximum.

Parhon and Parhon (29) reported that in the goose (of the race Rouen) the testis diminishes in volume about the first of August. The spermatogenic tissue then becomes less abundant, and its cells

divide less actively. The tubule cells are at this time charged with fat granules. The intertubular tissue is more developed than in spring, and the interstitial cells, like the tubule cells, are charged with fat granules. This condition resembles that reported by Champy for Amphibia.

Benoit (5 and 6) states that during the winter while the testis (of *Cambasson*) is in repose it contains spermatogonia and Sertoli cells. At the beginning of the sexual period in spring the seminiferous tubules enlarge a little. They slowly gain in volume as spermatogenesis increases. During the early period of development spermatocytes make their appearance, and then later spermatids are found. Only when *Cambasson* is fully active sexually are spermatozoa present, and at this time the testis is maximum in size.

He states that interstitial cells are very abundant during winter, when spermatogenesis has ceased. They then contain fat granules. Toward spring many connective tissue cells become enlarged. Some contain fuchsinophile spherules. When sex activity is at its height these interstitial cells are relatively much less abundant than during winter and early spring. They change in cytological structure, becoming, he thinks, glandular. He finds no volumetric parallelism between the interstitial cells and sex activity and endeavors to find a parallelism in the cytological changes seen at this time. These cytological modifications were briefly pointed out by Parhon and Parhon, but these authors were not led to believe that these cells were more secretory during the period of sex activity than during the inactive period. Many investigators are inclined to look upon these changes as showing that the interstitial cells are trophic bodies for the tubule cells. See Saintmont (33) and Tandler and Grosz (34). Others view them as consequences of changes in size of the tubules rather than from a teleological aspect. See Whitehead (40), Kuntz (24), Humphrey (21), and Oslund (28).

It is quite evident that sex activity in birds is pronounced during the period of spermatogenesis. At that time the testes are enlarged as compared with the inactive period. On the other hand there is an increase in the number and volume of interstitial cells during the period of sexual *in*activity. Plumage is usually more brilliant during the time that spermatogenesis is most active and is dull following the autumnal molt, when the interstitial cells are abundant. The parallelism between spermatogenesis and sexual activity is evident, while there is an inverse relationship between sexual activity and interstitial cells.

MODIFICATIONS IN TESTES OF MAMMALS

In testes of mammals the germinal epithelium is found in seminiferous tubules. Spermatogenesis proceeds in waves, and all of its stages may be found in each tubule. Between the tubules are found nerve elements, blood and lymph vessels, and connective tissue cells. Some of the connective tissue cells are typical fibroblasts, while others are large and contain an abundance of cytoplasm with fuchsinophile granules. It should be emphasized that not all connective tissue cells are interstitial cells, nor is the intertubular space always filled with interstitial cells nor even with fibroblasts. It often contains much lymph and always has blood and lymph vessels and nerve elements. Of all the intertubular tissue only the interstitial cells are supposed to elaborate a glandular product.

Hansemann (19) reported that in the Marmot (*Marmota marmota*) there is no trace of spermatogenesis during hiberna-

tion. There are at this time some interstitial cells, but they are not abundant. He found them abundant during the summer. Ganfini (17) repeated and extended the work on marmots. He found the interstitial cells as abundant in winter as in the sexually active season. He stated that they were more nearly round in winter and appeared to be secreting less actively.

Rasmussen (30) made a complete study of hibernation effects upon the testis in *Marmota monax*. From his data it seems that spermatogenesis progresses slowly during the late fall and winter months. In early March the spermatogenic activity increases markedly and reaches its height during the latter part of March and the first part of April. Thereafter spermatogenesis quickly subsides, and in June and July it is at its lowest point. From September on it again progresses slowly.

Interstitial cell hypertrophy starts just before mating, and the cells reach their maximum development after spermatogenesis has ceased and the tubules are empty. They remain well developed until July, at least two months after the cessation of the spermatogenic cycle. The mating season is during late March and early April, and young are born during the first part of May. Mating thus follows the great wave of spermatogenesis and precedes the crest of interstitial cell hypertrophy. See chart VI.

Regaud (31), Lecaillon (25), and Tandler and Grosz (34) have made a comprehensive study of the seasonal changes in the testis of the mole (*Talpa europea*). From their work it is evident that spermatogenesis proceeds in autumn and winter. The spermatogenic activity increases during late February and attains its height during March. At this time the testis is three times its usual diameter, and this increase results entirely from increase in germ cells. Rutting is during March, and by the end of the month most of the sperm are gone and the testis again decreases in size. Thereafter it reaches a low ebb in July, when only a syncytium of Sertoli cells and a few spermatogonia remain in the tubules. The interstitial cells are minimal during February and March. They increase immediately after mating, when the sperm are gone. When spermatogenesis again takes place in the fall the interstitial cells decrease, though they are still numerous during the winter according to Lecaillon.

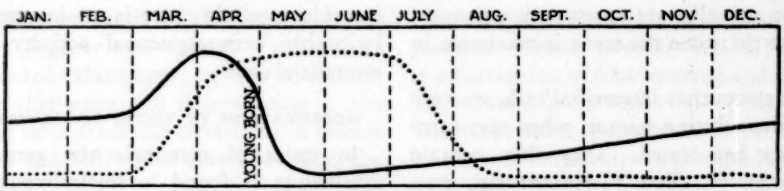


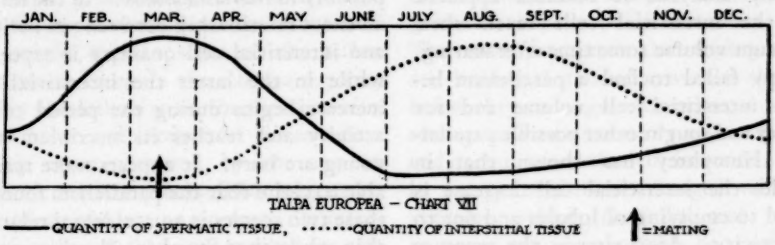
CHART VI MARMOTA MONAX

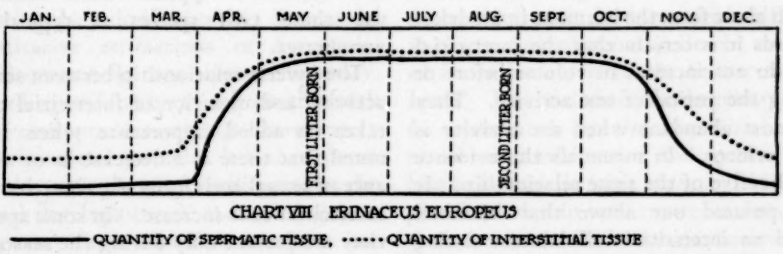
——— QUANTITY OF SPERMATIC TISSUE, ····· QUANTITY OF INTERSTITIAL TISSUE

In moles it is quite evident that interstitial cell hypertrophy occurs when spermatogenesis is minimal and the tubules empty. It does not precede mating but follows it. This is clearly shown in chart VII herewith presented.

According to Marshall (26) testes of the Hedgehog (*Erinaceus europeus*) begin to increase in size about the end of March, and by the middle of April they are

considerably enlarged. Active spermatogenesis is found in April, and free spermatozoa are present in the genital passages at the end of the month. Spermatogenesis continues until September, and from then on the testes decrease in size. According to this investigator the quantity of interstitial cells runs parallel with spermatogenesis. The increase in size of the testis, he says (26, p. 253) is due partly to the increase in the size and number of seminiferous tubules, but even more


JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SEPT. OCT. NOV. DEC.
TALPA EUROPEA – CHART VII
QUANTITY OF SPERMATIC TISSUE, ·····QUANTITY OF INTERSTITIAL TISSUE
=MATING


JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SEPT. OCT. NOV. DEC.
FIRST LITTER BORN
SECOND LITTER BORN
CHART VIII ERINACEUS EUROPEUS
QUANTITY OF SPERMATIC TISSUE, ····· QUANTITY OF INTERSTITIAL TISSUE

matogenesis. Part of the intertubular increase is due to the increase in the vascular bed, as Marshall has observed, but part appears to be due to interstitial cell increase. A study of the Hedgehog alone might lead one to infer that the interstitial hypertrophy paralleling spermatogenesis and sex activity had something to do with the increased sex activity of that period. Such an inference is not justified because this parallelism is not found in other species. Tandler and Grosz found that in the mole the only parallelism present is between spermatogenesis and sex activity. This parallelism is constant in all mammals. The quantity of interstitial cells in moles is at a minimum during sex activity, and in marmots they reach a maximum only after birth of young. This is long after mating has ceased. To function as activators of sex activity the interstitial cells should develop prior to or at the same time as spermatogenesis. As a matter of fact their increase follows sex activity.

to proliferation of interstitial cells. This results in wide separation of the tubules. Blood vessels of considerable size are not uncommon, but they disappear when retrogression sets in. Rasmussen states that there is an actual increase in the number of interstitial cells during part of the spermatogenic wave in marmots, which his chart shows reaches its maximum after mating. Spermatogenesis continues during the summer in the Hedgehog, and in this species the interstitial cell hypertrophy therefore parallels sper-

DISCUSSION

When the data on fishes are carefully assembled no correlation is found between the volume of the interstitial cells and time of sex activity. Such a parallelism was reported by Courrier, but Champy and Van Oordt have both shown this to be an error. In Amphibia such a parallelism was reported by Friedman and by Mazzetti for *Rana fusca*, *Rana viridis*, and *Hyla arborea*. When the data have been carefully analyzed it becomes apparent that the interstitial cells reach their maximum volume some time after mating. Champy failed to find a parallelism between interstitial cell volume and sex activity and sought other possible parallelisms. Humphrey has shown that in urodeles the interstitial cell increase is related to emptying of lobules and not to sex activity. Aron stresses the presence of Sertoli cells in the "Glandular masses" which alone form the hormone in urodeles. In birds it is certain that the interstitial cells do not increase in volume before or during the period of sex activity. They are most abundant when sex activity is least evident. In mammals the evidence is indicative of the same relationship. It was pointed out above that Marshall found an interstitial cell increase during spermatogenic activity in the Hedgehog. The interstitial cells increase before sex activity and decrease during hibernation. Rasmussen reported that in *Marmota monax* there is an increase of interstitial cells that begins before mating. But the interstitial cells are most abundant at the time of or after birth of the young. The maximum volume therefore lags behind actual mating rather than precedes it. Ganfini found that in *Marmota marmota* the interstitial cells were as abundant during winter as during the sexually active period. There is then no real parallelism between sex activity and interstitial cell volume in *Marmota*. In the mole it is certain that the interstitial cells are least abundant during the mating season. They increase when spermatogenesis is arrested, and this is after mating.

It is therefore clear that there is no constant parallelism between sex activity and interstitial cell quantity. In fact there is in most cases an inverse relationship. The only exceptions to this state of affairs are in *Erinaceus europeus* and possibly in *Marmota monax*. In the former an exact relationship between sex activity and interstitial cell quantity is reported, while in the latter the interstitial cell increase begins during the period of sex activity and reaches its maximum after young are born. It appears more reasonable to claim that the parallelism found in these two species is an accidental relationship while that found in all other species cited above is typical rather than to use these two species as typical of vertebrates.

The inverse relationship between sexual activity and quantity of interstitial cells takes on added importance when it is noted that there is a decrease in or abeyance of sexual activity at the time that the interstitial cells increase. In some species they are present only during the season of sex inactivity. Nor should their entire absence in certain species be overlooked. These facts stand in direct opposition to the interstitial cell secretory theory.

In the group of animals in which the interstitial cells are present only during the period of sex inactivity it might be argued that the hormone is effective only after a certain latent period. There are no data available that show how long it takes the hormone to become effective, but it is known that its absence is evident in 5 to 12 days in rats (Hoskins, 20) and in about the same period in birds when determined

by changes in feathering. The period between the disappearance of interstitial cells and the onset of sexual activity is so long that it seems improbable that the interstitial cells had any relation to sex desire and mating behavior.

It must be admitted that the methods of determining quantitative amounts of interstitial cells have not been accurate. This has been pointed out by Bascom (4). The authors have offered them as relative quantities and in such a sense they have shown the gross changes met with. One error is present throughout the early work that might explain some of the minor discrepancies seen in the various reports; namely the failure to distinguish between intertubular and interstitial tissue. Nor is this error corrected by the use of Bascom's method. It is difficult to make sure of estimating an increase in interstitial cell quantity and number in any way short of actually measuring and counting the individual cells. But careful quantitative estimations of interstitial cell increases do not appear necessary. According to Lipschutz (41) one-sixteenth of a testis produces enough hormone to keep the animal normal. It is also known that the testicular grafts will promote the normal development of male rats, guinea pigs, or birds. Small variations are therefore not important.

Are there cytoplasmic or nuclear changes paralleling the periods of sex activity that might indicate which cells secrete the testicular hormone? The change from fibroblast to interstitial cell is marked by the appearance of fuchsinophile granules in the cytoplasm and the inclusion of much fat. But this occurs during the post-active period according to the data reviewed above. Benoit found that the interstitial cells of *Cambasson* decrease in quantity during the season of sex activity, but he believes that they become more glandular at this time. They contain voluminous spherules which produce a fuchsinophile secretion. The supporters of the interstitial cell secretory theory, after noting what they thought was a parallelism between sex activity and interstitial cell increase, postulated that these cytoplasmic inclusions were the hormone products being formed in the cells. No proof has been offered in support of this supposition. Now Benoit and others turn about and postulate that since certain cells contain fuchsinophile granules they must be secretory cells. They must first prove that such granules are hormonal products within the cell before they can argue that cells containing such granules are secretory cells. Parhon and Parhon noted that the interstitial cells in the goose become charged with fat granules, which they believed to be secretory material, but this occurs in the fall after mating has ceased. Champy found changes in the interstitial cells and in the Sertoli cells that indicated transfer of fat inclusions from the former to the latter. He concluded that the phosphorus fat elaborated by the interstitial cells serves as nutrition for the spermatozoa being formed in this tissue. He then postulates that in some mysterious manner the interstitial cells determine the development of the germ cell, presumably through the transfer of this secretory (fatty) material. Humphrey has very clearly shown that interstitial cell increase is related to emptying of spermatic tubules and that it is not a seasonal condition. Humphrey suggests that they may serve as a nutritional balance in the testis and also prevent a sudden collapse of the lobules and of the testis when sperm are ejected. Oslund (28) suggests that they are more strictly a result and ascribes to them no functional purpose.

The writer interprets Champy as stating

that in some anurans the interstitial cells produce the testicular hormone. But where prespermatogenesis is found the hormone is produced by this abortive spermatogenesis. In urodeles he believes that the hormone is produced by a "corpus jaune testiculaire," which is a product of the abortive spermatogenic process. Aron maintains that a "glandular body," which he describes as a product of Sertoli cell division, produces the testicular hormone in urodeles. Both of these authors therefore point to germinal elements as the chief source of the hormone production. Their individual theories are very much weakened by Humphrey's observations, which indicate that this abortive spermatogenesis in American urodeles is a result of unfavorable environment, that it is not present in many species and in those species where it is sometimes seen it is not constant. We cannot call this a parallelism but a coincidence, for which Humphrey has offered a satisfactory explanation.

There is, however, one parallelism that is constant in all species. A glance at the charts will make it apparent that there is always an abundance of germ cells, either developing or mature, immediately before and during mating. In all animals there is some germinal tissue throughout the year. It increases slowly after mating and becomes abundant when the next mating season approaches. In some species the increase immediately before mating is rapid, while in others it is more gradual. These are individual variations of cell activity, but in all vetebrates the germinal tissue is maximum in quantity at the time of mating. This of itself does not show that this tissue produces the testicular hormone. Spermatogenesis is the preparation of cells whose function is that of fertilizing the egg. But may not these anatomic and physiologic changes of mating be induced by a substance produced by the metabolic processes of these cells? This substance may be a waste product of cell metabolism or a by-product (an unused material) split off from the material furnished to the cell by the blood. We know, for example, that the lymph from the arm or leg differs from that of other parts of the body. This appears to be a result of the cell metabolism of the particular tissue concerned.

Germ-cell development is the only parallelism at present found between any particular testicular element and the physiological changes accompanying mating. Champy (10) states that though there is no positive demonstration there is presumptive evidence favoring a correlation between appearance of sex characters and maturity of spermatozoa in *Cysprinodentes varions*. The writer is not ready to commit himself to such a definite correlation. It seems that the presence of any *active germinal epithelium* is sufficient to insure what is commonly thought of as hormonal activity.

The charts for this paper were made in the Illustration Studios of the University of Illinois College of Medicine and Dentistry.

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EVOLUTION AND MORTALITY

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THE PROBLEM

IN 1920, in an attempt to approach the problem of human mortality from a more rational standpoint than that of current vital statistics, I (8) discussed the distribution of human deaths on the basis of an organological classification of the several statistically recorded causes. The underlying idea in the classification was to group all causes of death under the heads of the several organ systems of the body, the functional breakdown of which is the immediate or predominant cause of the cessation of life. The basis of the classification was not that of etiology, but rather that of the anatomical location of the principal breakdown. The matter was further discussed and the original classification amended and corrected in later publications (9, 10).

In these investigations there came to light evidence that the present characteristics and distribution of human mortality are in part—perhaps a considerable part—the results or consequences of the evolutionary history of the human body itself. It appeared that the different organ systems of the body are not all equally capable of withstanding the environmental stresses and strains which they have to meet. The evidence on this point was necessarily suggestive rather than conclusive. Human vital statistics, taken by themselves, are for many reasons inadequate to elucidate such a point as this. It demands a study of the evolutionary progression which has occurred in respect of mortality among the animals lower in the scale than man, who represents only the final end term in the series. The real question, on which we should like to have evidence is: How do the relative mortalities chargeable to breakdown of each of the different organ systems of the body compare among the different orders of animals, including man?

What obviously is needed to answer the question is a record of the comparative pathological anatomy of the different orders of vertebrate animals. Unfortunately there does not exist anything like a complete or detailed body of knowledge regarding the pathology of wild vertebrate animals living in a natural state. There are several reasons for this lack, besides the obvious one that few persons have particularly interested themselves in such study. The wild animals that happen to be killed by hunters are the survivors of a steady process of natural selection, and are therefore apt to be in an excellent state of health. The sick, weak and defective have long since died off, under circumstances practically always making impossible post-mortem examination. Again wild animals probably only rarely die a natural death due to internal pathological changes. When an animal in a state of nature falls appreciably below par in health, sooner or later something kills it.

MORTALITY IN ZOOLOGICAL GARDENS

But while ideal material for comparative pathology is thus lacking, there is available a body of records which can be utilized to throw some light on our problem. I refer to the autopsy records made in large zoological gardens. The important conditioning factors regarding such records from a biometric point of view are these:

a. The population of a zoological garden is composed of wild animals. But in this population the different natural orders are not necessarily or actually represented in proportion to the frequency with which individuals belonging to these orders occur in a state of nature. The population is a selected one, the basis of the selection being primarily the behavior and longevity of the individuals in captivity, and their interest to human beings as objects of display. This artificial character of a zoological garden population means that deductions regarding mammals as a group, or birds as a group, must always be subject to the reservation that the samples are not completely representative.

b. The animals are in a state of captivity, artificially and regularly fed, in accordance with what human beings, on an insufficient basis of knowledge, suppose to be their needs and desires. That these conditions alter the whole natural and normal biological picture, including its pathological aspects, admits of no doubt. To paraphrase Dr. Johnson's remark about the performing dog the wonder is not that the animals live as well as they do in zoological gardens, but that they live at all under such unnatural circumstances.

c. In most zoological gardens complete and careful post-mortem examinations are not made of all the animals that die, and the results of such examinations as are made are not published in detail. An outstanding exception to the latter statement is furnished by the thorough and painstaking work of Fox (2) and his assistants at the Philadelphia Zoological Garden. Here a trained pathologist has taken the work seriously and amassed a collection of records of great interest and value. It is unfortunate that the statistical presentation of the records in the monumental report cited falls, in some respects, below the high level of excellence of the pathological work itself.

While these factors distinctly limit the usefulness, for the present purpose, of these records of deaths in zoological gardens, it is desirable to examine some of them briefly. In a comprehensive study of the biology of life duration and death any and all evidence, however fragmentary, should be brought under review.

DATA FROM THE LONDON ZOOLOGICAL GARDEN

From a biometric point of view the statistics of deaths in the Garden of the Zoological Society of London, are the most satisfactory. Their outstanding merit is that they account, in some way or other, for *all* the deaths occurring within a given year. The record is statistically complete. It is in this respect that the death records from the National Zoological Park in Washington, published in the Annual Reports of the Smithsonian Institution, fail. In a quite erratic way they leave a considerable number of deaths unaccounted for.

The present paper is based upon the statistics from the London Gardens for the four years 1920 to 1923 inclusive, as published by N. S. Lucas, M.B., F.Z.S. (4–7), the pathologist to the Society during the years named.

In these four years 4,448 deaths in total were reported. Of these 3,150 were recorded by causes, as determined by

autopsy, for mammals, birds, and reptiles. The remainder fell into Class X (*cf. infra*), incapable of organological classification. Individuals not autopsied are accounted for under such rubrics as "Eaten by rats;" "Decomposed;" "Not examined." Besides these there is the rubric "Killed," which includes those animals killed by other animals. Those killed on order, because of illness or for other reasons, are distributed to causes according to the results of the autopsy examination. Other rubrics are "Not diagnosed;" "Exposure." The number of deaths under these and other organologically unclassifiable rubrics, such as "Debility," is large in the case of reptiles, less in birds, and much smaller in the mammals. In dealing with the material one is obliged to assume that these deaths constitute in part a random sample, in respect of pathological causation, of all deaths; or, in the case of purely accidental deaths, are of entirely healthy individuals. In the second of these alternatives the deaths obviously have no place in a *biological* classification. They simply do not come into the reckoning here, any more than with human mortality. As to whether the other organologically unclassifiable deaths are a random sample, pathologically speaking, of the total it is impossible to determine definitely. It seems probable that they are fairly so, for the reason that if one compares the statistics of different zoological gardens, in which the proportions of unautopsied or unrecorded deaths vary widely, it is found that the ratios between the different ascertained causes among the autopsied and recorded portion of the dead population are fairly constant from garden to garden. This could only happen, assuming honest and fairly careful autopsy work, as we are entitled to, if the unrecorded deaths approximated a random sample of all deaths in respect of their pathological characteristics.

The organological classification of the causes of death set up in (8–10) and followed in this present study is as follows:

I. Circulatory system, blood, and blood-forming organs.
II. Respiratory system.
III. Primary and secondary sex organs.
IV. Kidneys and related excretory organs.
V. Skeletal and muscular systems.
VI. Alimentary tract and associated organs concerned in metabolism.
VII. Nervous system and sense organs.
VIII. Skin.
IX. Endocrinal system.
X. All other causes of death.

TABLE 1

Deaths in London Zoological Garden, 1920–1923 inclusive

YEAR	MAMMALS		BIRDS		REPTILES	
	I-IX	X	I-IX	X	I-IX	X
1920	273	63	369	103	148	113
1921	169	38	392	121	163	109
1922	261	58	434	147	119	107
1923	241	90	443	196	138	153
Totals	944	249	1,638	567	568	482

The actual numbers of the 4,448 deaths in the London Zoological Garden, here dealt with, falling respectively into Classes I–IX inclusive, and Class X, are shown in table 1.

ORGANOLOGICAL DISTRIBUTION OF DEATHS

In table 2 the biologically classifiable deaths in the four years experience (1920–1923) of the London Zoological Garden are tabulated according to organ systems, on a percentage basis, the figures representing the number of deaths in each class per hundred deaths from all causes (exclusive of those falling in our Class X). For comparison the last two columns give corresponding figures for human beings. The first of these columns is from the mortality of the City of São Paulo, Brazil, in 1917, and the second from that of

England and Wales in 1914. England stands at the forefront of civilization in general and of health, hygiene and sanitation in particular. Man in England represents certainly a high product of human evolution. The population of São Paulo is, statistically speaking, a more primitive one, from both a general evolutionary viewpoint and from that of public health and sanitation, than that of England and Wales. To take but a single example by way of evidence in support of this statement, the official records state that 18.2 per cent of the persons married in the City of São Paulo during the year 1918 were illiterate (unable to read or write).

In one respect the figures in the last two columns of table 2 differ from those previously published (8, 9 and 10) for the same population. In the original treatment of the human material on the basis of organological classification of the mortality a portion of the deaths of infants recorded as due to "premature birth" and to "injuries at birth" were included with the deaths falling in Class III, Primary and Secondary Sex Organs. The reasons for so assigning those deaths were fully discussed in the publications cited. But plainly there is nothing in the mortality of lower animals, as recorded in zoological gardens, which corresponds to the infant mortality. So then the deaths due to these causes were subtracted out of the totals of Class III in making up the last two columns of table 2. The residue is more nearly comparable with the mortality placed in this class in the case of the lower animals.

The first thing which strikes one, upon examining this table, is that broadly the distribution of mortality to organ systems runs parallel in the three orders of lower animals to the condition found in man. This is shown graphically in figure 1.

It is seen at once that in reptiles, birds, and mammals, just as in man, the two organ systems having the largest mortality chargeable to them are the respiratory and the alimentary systems, with the circulatory system standing third. The other organ systems, which have a low mortality chargeable to them in man, also are concerned in a low mortality in the reptiles, birds, and mammals. This rough, but still evident correspondence between man and the lower orders of vertebrates in the organological distribution

TABLE 2

The distribution among the different organ systems of each 100 biologically classified deaths

GROUP NUMBER	ORGAN SYSTEM	REPTILES	BIRDS	MAMMALS	MAN (SÃO PAULO 1917)	MAN (ENGLAND AND WALES 1914)
I	Circulatory system, blood	4.75	3.85	6.99	18.78	25.57
II	Respiratory system	32.99	37.33	46.19	26.94	33.44
III	Primary and secondary sex organs	2.11	2.87	0.64	2.22	3.86
IV	Kidneys and related excretory organs	0.88	4.52	3.92	5.29	4.03
V	Skeletal and muscular system	0	0.37	2.01	0.44	1.54
VI	Alimentary tract and associated organs	58.56	50.83	38.66	39.22	21.40
VII	Nervous system and sense organs	0	0.12	0.64	6.52	8.91
VIII	Skin	0.70	0	0.32	0.51	1.01
IX	Endocrine system	0	0.12	0.64	0.07	0.23
	All biologically classified deaths	99.99	100.01	100.01	99.99	99.99

of their mortality considerably tends to increase one's confidence that this classification of mortality has some real biological significance.

This confidence is further increased if table 2 is studied in detail. Let us consider first Class II, the mortality attributable to breakdown of the respiratory system. It is seen that this mortality steadily and regularly increases proportionately as we pass from reptiles, through birds, to mammals. There appears to be a clear evolutionary progression here. The respiratory system of mammals appears to be less effectively adapted for coping with the environmental stresses and strains put upon it than it is in reptiles. When we come to man this progression is broken. Respiratory mortality is here lower. The thought at once suggests itself that here is to be observed a result of man's intelligent control of his environment through housing, sanitation, and hygiene. It is at least conceivable that man's real biological position here should be with a respiratory mortality as high or higher than that of the lower mammals. But because he has learned in some degree how to protect himself from respiratory infections, and to treat them so that they do not so often lead on to death, his actual observed respiratory mortality falls somewhat below that of the lower vertebrate orders.

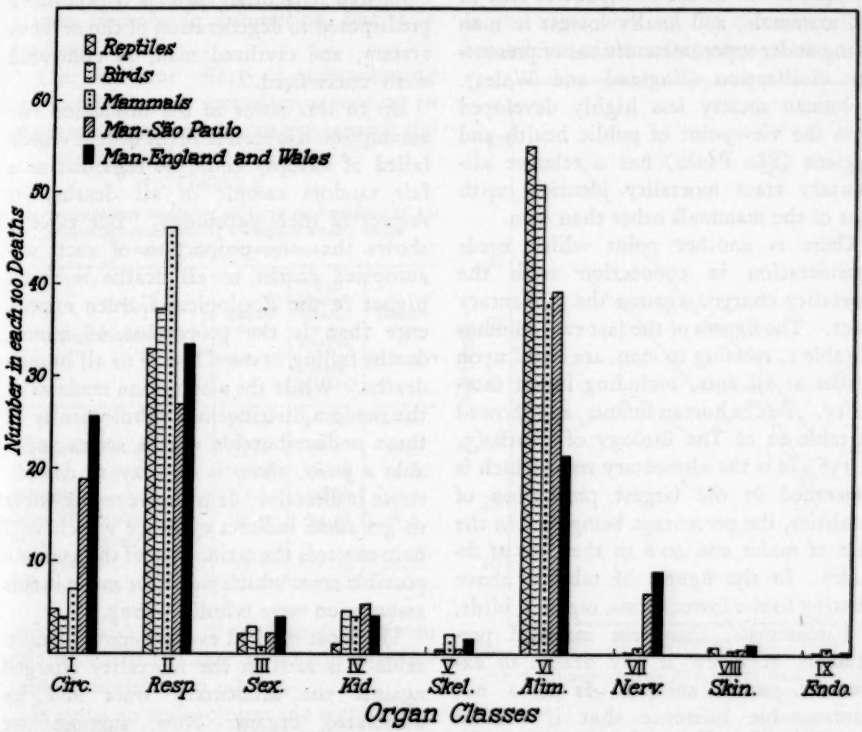

FIG. 1. THE MORTALITY, PER HUNDRED DEATHS FROM ALL CAUSES, DISTRIBUTED AMONG NINE ORGAN SYSTEMS, IN REPTILES, BIRDS, MAMMALS, AND MAN

If the mortality chargeable to the alimentary tract and its associated organs is examined in detail there is again seen to be a regular progression associated with advancing phylogenetic position. The proportionate mortality from diseases finding their seat in the alimentary tract and its associated organs is highest in the reptiles, lower in the birds, lower still in the mammals, and finally lowest in man living under superior conditions of present-day civilization (England and Wales). A human society less highly developed from the viewpoint of public health and hygiene (São Paulo) has a relative alimentary tract mortality identical with that of the mammals other than man.

There is another point which needs consideration in connection with the mortality charged against the alimentary tract. The figures of the last two columns of table 2, relating to man, are based upon deaths at all ages, including infant mortality. But in human infants, as I showed in table 11 of The Biology of Death (9, p. 136), it is the alimentary tract which is concerned in the largest proportion of fatalities, the percentage being 68.8 in the case of males and 40.6 in the case of females. In the figures of table 2 above relating to the lower forms, reptiles, birds, and mammals, there are included presumably very few if any deaths of extremely young animals. It is a not unreasonable inference that if "infant mortality" were included in the figures for animals the proportionate mortality chargeable to the alimentary tract would be even higher in reptiles, birds, and mammals than the figures actually available indicate.

There is a regular progression of increasing mortality chargeable to the nervous system as we go up the evolutionary scale, and the same thing appears to be true for the excretory organs, with some minor fluctuations in the figures not greater than might reasonably be expected by chance, where the numbers involved are so small. The tendency to increasing mortality from breakdown of the nervous system was long ago noted by Laycock (3) in his lectures on constitution in relation to disease. He said (p. 206): "Man as compared with other animals is peculiarly predisposed to degeneration of the nervous system; and civilized man, as compared with uncivilized."

Up to this point in the discussion the assumption has been that the deaths which failed of autopsy could be regarded as a fair random sample of all deaths, in respect of their pathology. But table 1 shows that the proportion of such unautopsied deaths to all deaths is much higher in the Zoological Garden experience than is the proportion of human deaths falling in our Class X to all human deaths. While the assumption made as to the random distribution pathologically of these undistributable deaths seems probable *a priori*, there is no way to demonstrate it directly. It is, however, possible to get some indirect evidence which will help towards the estimation of the extreme possible error which would be made if this assumption were wholly wrong.

The most marked evolutionary trend in table 2 is seen in the mortality charged against the alimentary tract and its associated organs. Now suppose we make the two possible assumptions which will set the extreme limits of the effect which could be produced by altering the distribution of the organologically unassignable deaths of Class X.

I. The first of these assumptions is that

$$\text{All X} = \text{VI},$$

that is, that all the deaths now in Class X were in fact due to breakdown of the alimentary tract and its associated organs.

This is obviously a biologically improbable assumption, but limiting assumptions often are highly improbable.

II. The second assumption is that

No X = VI

that is, that no death now in Class X was due to lesions of the alimentary tract or its associated organs. This again is a highly improbable assumption, but it is limiting.

The resultant effect of redistributing the proportionate mortality according to these two assumptions, together with the initial assumption of random distribution of the deaths in Class X, which underlies table 2, is shown in table 3.

TABLE 3

The proportionate mortality assigned to breakdown of the alimentary tract and its associated organs, under each of three assumptions

ANIMAL GROUP	ASSUMPTION I ALL X = VI	X IS RANDOM SAMPLE OF ALL DEATHS. (DATA FROM TABLE 2)	ASSUMPTION II NO X = VI
	per cent	*per cent*	*per cent*
Reptiles	77.6	58.6	31.7
Birds	63.5	50.83	37.8
Mammals	51.5	38.66	30.6
Man, São Paulo	43.3	39.22	36.9
Man, England and Wales	29.8	21.40	19.1

In order to make clearer the significance of the data of table 3, figure 2 has been prepared.

It is seen that the trend of the mortality under Assumption II is, as a whole, slightly downward if man in England and Wales be taken into account. Leaving this last point out of consideration the trend under Assumption II is nearly horizontal. But under the limiting Assumption I the trend is plainly downward. The true facts must fall somewhere between I and II. Hence the conclusion seems to be that, however the unassignable mortality of Class X may be supposed to be distributed, there has been a steadily decreasing proportion of the total mortality due to breakdown of the alimentary tract during the evolutionary progression from reptiles to man.

The limiting assumptions were applied in the same way to the mortality from breakdown of the respiratory system, with the similar result of showing that the evolutionary trend of the mortality assignable to this system has been, in greater or smaller degree, in the *direction* indicated in table 2.

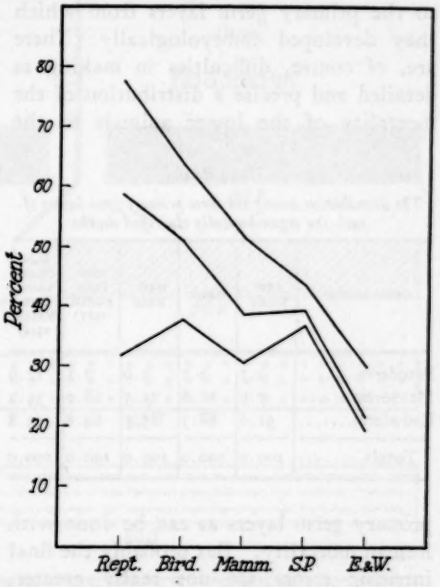

FIG. 2. TREND OF THE MORTALITY ASSIGNED TO CLASS VI, UNDER THREE ASSUMPTIONS

It would seem, then, that even though the anatomically unassignable mortality in the London Zoological Garden material is absolutely larger than is desirable, still the element of uncertainty that is thereby introduced into our conclusions pertains

rather to the *rate* of the evolutionary changes in mortality, than to their *sense* or direction.

THE PRIMITIVE GERM LAYERS AND MORTALITY

One obvious advantage of the organological classification of mortality is that it permits the final grouping of deaths into three large classes, based upon the assignment of the different organs of the body to the primary germ layers from which they developed embryologically. There are, of course, difficulties in making as detailed and precise a distribution of the mortality of the lower animals to the primary germ layers as can be done with human mortality. But probably the final intrinsic errors are not really greater, because the greater accuracy of the diagnoses based on autopsies in the lower animals, as compared with the general vital statistics of human beings based merely upon the physicians' opinion as to the cause of death, probably offsets the other deficiencies in the material. In any case I think the results presented in table 4 may be regarded as at least an approximation to the true facts.

TABLE 4

The distribution among the three primary germ layers of each 100 organologically classified deaths

GERM LAYER	REPTILES	BIRDS	MAMMALS	MAN (SÃO PAULO 1917)	MAN (ENGLAND AND WALES, 1914)
Ectoderm.....	0.7	0.1	1.0	7.2	11.0
Mesoderm.....	7.7	11.6	13.5	28.0	35.2
Endoderm.....	91.6	88.3	85.5	64.8	53.8
Totals.....	100.0	100.0	100.0	100.0	100.0

The orderly character of the data in table 4 is striking. Proceeding up the evolutionary scale from the extreme left hand column of the table (Reptiles) to the extreme right hand column (Man in England) the proportionate mortality from breakdown of organs developing from the ectoderm, and from the mesoderm, *increases*, while the proportionate mortality associated with organs which develop from the endoderm *diminishes*.

These figures are shown graphically in figure 3.

DISCUSSION

In the initial discussion of the organological classification of mortality the following statement was made (10, pp. 168 and 169):

> "Taking a general view of comparative anatomy and embryology it is evident that in the evolutionary history through which man and the higher vertebrates have passed it is the ectoderm which has been most widely differentiated from its primitive condition, to the vitality of which statement the central nervous system furnishes the most eloquent evidence. The endoderm has been least differentiated in the process of evolution, while the mesoderm occupies an intermediate position in this respect. An elaborate array of evidence might be presented on these points, but to do so would be supererogation. It would amount simply to repeating any standard treatise on the comparative anatomy of the vertebrates.
>
> "From the present point of view we see that the germ layer, the endoderm, which has evolved or become differentiated least in the process of evolution is least able to meet successfully the vicissitudes of the environment. The ectoderm has changed most in the course of evolution. The process of differentiation which has produced the central nervous system of man had as a concomitant the differentiation of a protective mechanism, the skull and vertebral column, which very well keeps the delicate and highly organized central nervous system away from direct contact with the environment. The skin exhibits many differentiations of a highly adaptive nature to resist environmental difficulties. It is then not surprising that the organ systems developed from the ectoderm break down and lead to death less frequently than any other."

These inferences were drawn from an examination of the evidence from human

mortality alone. Now we have at hand in tables 2 and 4 of the present paper some additional evidence. We see at once that all along the evolutionary pathway, from reptiles to man, the endoderm has had the largest absolute mortality chargeable against it, but the *proportionate* amount has steadily diminished. It is a possible inference from the evidence that the organs derived from endoderm have become progressively better adapted to meeting successfully the environmental stresses and strains which bear upon them in the business of living.

On the other hand the proportionate mortality assignable to the organs derived from the ectoderm and the mesoderm has increased in the course of evolution. There is, of course, a necessary compensation in this. If 100 per cent of mortality is divided into parts and some of these parts exhibit a secular change, up or down, the other parts must of necessity show a trend in the opposite sense. If preventive medicine has in any degree reduced the *proportionate* number of deaths associated with the endodermal organs, just by so doing it must necessarily have increased the *proportionate* mortality associated with either ectodermal or mesodermal organs, or both. But it should not be overlooked that the same trends

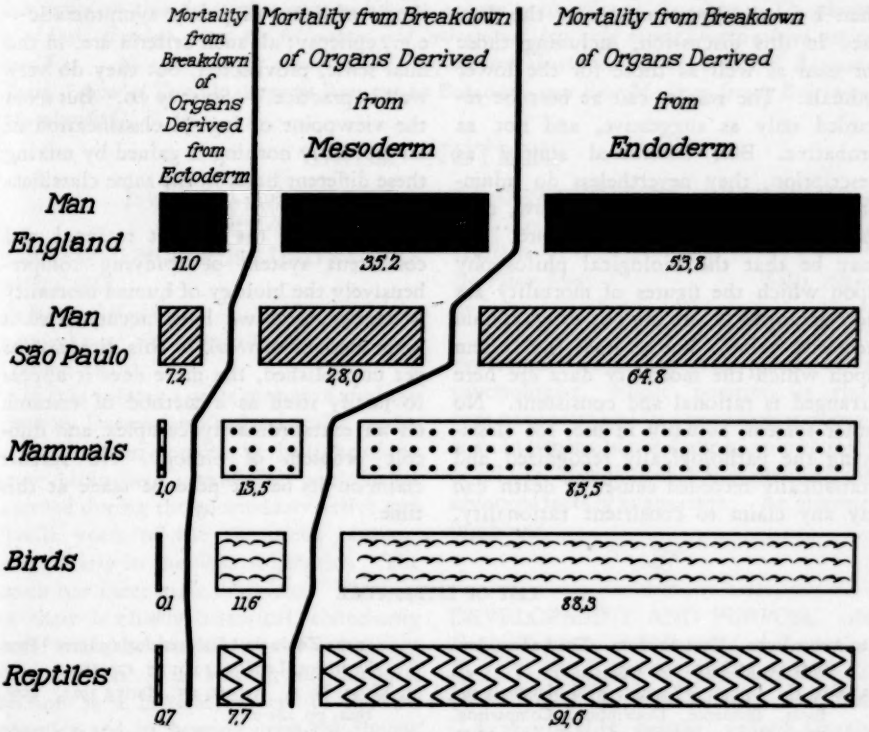

FIG. 3. THE MORTALITY, PER HUNDRED DEATHS FROM ALL CAUSES, DISTRIBUTED ACCORDING TO THE PRIMARY GERM LAYERS FROM WHICH THE DIFFERENT ORGAN SYSTEMS DEVELOP EMBRYOLOGICALLY

are observable in the proportionate mortalities of ecto, meso, and endodermal organs before man and preventive medicine are reached. So perhaps this art and science has only altered the course of evolutionary events quantitatively, and not qualitatively.

In conclusion I should like to say that no one can possibly recognize more clearly than I do the shortcomings of the data used in this discussion, including those for man as well as those for the lower animals. The results can at best be regarded only as suggestive, and not as probative. But, considered simply as description, they nevertheless do adumbrate another, and, so far as I know, new example of the "order of nature." It may be that the biological philosophy upon which the figures of mortality are here arranged is not the one of maximum heuristic value. But at least the system upon which the mortality data are here arranged is rational and consistent. No other system, actually in use, for classifying the pathologically recognized and statistically recorded causes of death can lay any claim to consistent rationality. The official "International List" for the classification of the causes of death shifts its basis, within its titles, with complete casualness and abandon between etiology, organology, embryology, and mere symptomatology. As was recently (1) pointed out in *The Lancet:* "The useful definition of a disease may be aetiological—e.g., typhoid fever—or anatomical—e.g., cirrhosis of liver—or purely symptomatic—e.g., epilepsy; all such criteria are, in the final sense, provisional, but they do very well in practice." So they do. But from the viewpoint of logical classification of all mortality nothing is gained by mixing these different bases in the same classificatory scheme.

The further the present rational and consistent system of studying comprehensively the biology of human mortality is carried, and we have accumulated a large amount of work in this direction as yet unpublished, the more does it appear to justify itself as a method of research on an extraordinarily complex and difficult problem of biology. No further claim on its behalf need be made at this time.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only meons that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

ABSTAMMUNGSLEHRE UND NEUERE BIOLOGIE.
By Richard Hertwig. *Gustav Fischer*
14 marks 7 x 10; 271 (paper) *Jena*
(Bound 16 marks)

In this volume a great master of zoology reviews Darwinism, and critically evaluates its present position in the light of the new biological knowledge which has accrued during the enormously active and fertile years of the twentieth century, particularly in the field of genetics. The book has three main divisions. The first of these is chiefly historical, concerning itself with the development of the theory of evolution. The second, and longest, section is a critical review of modern genetics and its bearing upon the theory of evolution. The last section of the book is concerned with phylogeny, chiefly from the viewpoint of critically considering the kinds of evidence which will lead to sound knowledge in this field. Altogether it is a stimulating and valuable contribution, the usefulness of which to the student is unfortunately diminished by the fact that it contains no bibliographical documentation whatever.

LA DESCENDANCE. *L'hérédité. L'origine des caractères. La fécondation. La vieillesse.*
By Pierre-Jean. *Félix Alcan*
15 francs 5⅝ x 9; 238 (paper) *Paris*

A philosophical discussion of life and evolution, from the viewpoint of a psychologist, whose position is that consciousness (and its derivative, memory) is an indispensible and irreducible element of all life, alone capable of explaining the observed facts of adaptation. An interesting book.

DEVELOPMENT AND PURPOSE. *An Essay Towards a Philosophy of Evolution.*
By L. T. Hobhouse. *The Macmillan Co.*
$6.00 5½ x 8½; xxxix + 494 *New York*

A thoroughly revised, indeed largely rewritten, edition of a book that has long been a classic of modern philosophy. The general conclusion is unchanged, that the world process is "a development of organic harmony through the extension of control by Mind operating under mechanical conditions which it comes by degrees to master. The empirical synthesis is in the main limited to the history of mind upon this earth, and to the stages by

which intelligence makes for itself a vehicle in the physical organism. The deductive argument exhibits this process as a part of a vaster and more significant evolution. But the strength of the position is that, so far as the two arguments cover the same ground, they coincide in the main lines of their teaching."

TRAVELS IN SPAIN AND THE EAST. *1808–1810.*
By Sir Francis Sacheverell Darwin.
The Macmillan Co.
$2.40 5 x 7½; ix + 121 *New York*

Sir Francis Sacheverell Darwin was the sixth son of Erasmus Darwin. In 1808 he set out from Birmingham to see the world with Mr. Theo. Galton, Francis Galton's uncle, and three other companions. This book is his diary for the next two years. It is delightful reading. They had plenty of adventures, and saw a great many interesting things in a trip which took them as far east as Constantinople. Of the original party one is robbed and murdered on the road, soon after they land in Spain; a second goes to the bottom in the Viper between Cadiz and Gibraltar; a third joins the army and is killed on the retreat to Corunna. Finally Mr. Galton gets the plague in Malta and dies, Mr. Darwin staying with him to the end.

The book is a welcome addition to Darwiniana and Galtoniana.

GENETICS

THE GENETICS OF SEXUALITY IN ANIMALS.
By F. A. E. Crew. *The Macmillan Co.*
$4.00 5½ x 8½; + 188 *New York*

This book, which is published in the *Cambridge Comparative Physiology* series covers, in greater detail, similar ground to that reviewed in THE QUARTERLY REVIEW OF BIOLOGY in the articles by Professor Crew which appeared last year. The material is discussed under the following heads: The mechanism of sex-determination; the physiology of sexual differentiation; sex-reversal in the adult individual; the mode of inheritance of sex-dimorphic characters; and the sex-ratio. There are very extensive and complete bibliographies. The book will be extremely valuable as a reference source for the development of knowledge up to the present time in what is just now one of the most lively fields of biological research.

THE HARVEST OF THE YEARS.
By Luther Burbank with Wilbur Hall.
Houghton Mifflin Co.
$4.00 5½ x 8; xxvi + 296 *Boston*

Essentially an autobiography of an interesting human being, though largely written in actual fact by Mr. Hall after Mr. Burbank's death, but with the aid of copious notes which he had left. Every student of genetics will be interested in reading this volume, particularly between the lines. It is illustrated with some twenty odd photographs, chiefly portraits of Mr. Burbank and his friends. The book is a fine record of a useful life. It lacks an index.

A RÉSUMÉ OF CATTLE INHERITANCE.
By John W. Gowen. *Martinus Nijhoff*
2.60 guilders *The Hague*
6¼ x 9¾; 54 (paper)

A thorough review, with a bibliography of 156 titles, of the present state of knowledge regarding inheritance in domestic

cattle. The genetics of more than thirty characters has been studied. Dr. Gowen's own outstanding work in this field makes him the person of choice to do such a comprehensive and critical review as this.

GENETICS OF DOMESTIC CATS.
By Ruth C. Bamber (Mrs. Bisbee).
Martinus Nijhoff
4.40 guilders *The Hague*
$6\frac{1}{4}$ x $9\frac{3}{4}$; 86 (paper)

The domestic cat has furnished some entertaining genetic puzzles. It is a valuable service which Mrs. Bisbee has performed in bringing together and critically reviewing all the scattered literature in the field. She says that the problem of the tortoise-shell male "is by no means settled."

MENDELISM.
By Reginald C. Punnett. The Macmillan Co.
$3.00 $4\frac{7}{8}$ x $7\frac{5}{8}$; xv + 236 *New York*

The seventh edition of one of the earliest and best popular expositions of the principles of Mendelian inheritance. The chief alterations in the revision relate to Goldschmidt's work on intersexes, and the chromosome theory of genetic phenomena.

GENETISCHE ANALYSE VAN KLEUREN, VEERPATRONEN, TINTEN EN AFTEEKENINGEN BIJ POSTDUIVEN.
By C. J. A. C. Bol. *Martinus Nijhoff*
5 guilders *The Hague*
$6\frac{5}{8}$ x $9\frac{7}{8}$; 108 (paper)

A detailed account of an investigation of the genetics of color and pattern in the plumage of carrier pigeons. There is a bibliography of twenty titles.

GENERAL BIOLOGY

AUS DEM LEBEN DER BIENEN.
By K. v. Frisch. *Julius Springer*
4.20 marks $4\frac{5}{8}$ x $7\frac{1}{4}$; x + 149 *Berlin*

DIE LEHRE VON DER VERERBUNG.
By Richard Goldschmidt. *Julius Springer*
4.80 marks $4\frac{5}{8}$ x $7\frac{1}{4}$; vi + 217 *Berlin*

EINFÜHRUNG IN DIE WISSENSCHAFT VOM LEBEN ODER ASCARIS. *2 vols.*
By Richard Goldschmidt. *Julius Springer*
8.80 marks for 2 vols. *Berlin*
$4\frac{5}{8}$ x $7\frac{1}{4}$; xi + 340

The first three numbers in a new series of popular scientific treatises, having the general title *Verständliche Wissenschaft.* The books are very attractively printed and bound, abundantly and well illustrated. So far as one may judge from the first numbers, the intrinsic merits of the series would seem to warrant the prediction of a considerable success for it.

The first volume gives the best account of the biology of the honey bee that we have seen in equal space. A great deal of attention is devoted to the experimental work which has been done on the behavior of the bee.

The first of the volumes by Professor Goldschmidt is an exposition of the present state of knowledge of genetics. The second, in two volumes, is a wide-ranging discussion of adaptation in the animal world. Both are extremely well done. The latter appeals to us especially as a fine piece of literary work, calculated to excite the interest and hold the attention of the general reader, to a degree rarely attained in popular scientific writing.

ANIMAL ECOLOGY.
By Charles Elton. *The Macmillan Co.*
$4.00 $5\frac{1}{4}$ x $8\frac{1}{2}$; xx + 207 *New York*

An interesting and original treatise on ecology, which from the author's point of

view "simply means scientific natural history." This attitude towards the subject is in refreshing contrast to that of some American workers in this field, who, in their zeal to be up-to-date and strictly in the mode, appear to regard ecology as a branch of physics. Mr. Elton discusses the subject under the following heads: The distribution of animal communities; ecological succession; environmental factors; the animal community; parasites; time and animal communities; the numbers of animals; variations in the numbers of animals; dispersal; ecological methods; ecology and evolution. There is a bibliography of 152 titles on the general subject, and a number of specific references to systematic works on British animals. Altogether this is a valuable contribution to the literature of general biology.

Professor Julian Huxley contributes an introduction.

LEBEN. ALTERN. TOD.
By E. Korschelt, S. Hirsch, F. W. Harms, M. Hartmann and H. Driesch.
Hugo Bermühler
2.50 marks *Berlin-Lichterfelde*
7 x 10; 81 (paper)

A collection of five lectures, by the authors named, given in Frankfurt in 1925–26. Prof. Korschelt deals with duration of life in animals and plants; Dr. Hirsch with the phenomenon of senescence and death; Dr. Harms with rejuvenation and the prolongation of life; Dr. Hartmann with death, reproduction and rejuvenation, with special reference to the protozoa; and finally Prof. Driesch with life, death and immortality. The treatment is in all cases popular in style. There is no index.

HIPPOKRATES. *Eine Auslese seiner Gedanken über den gesunden und kranken Menschen und über die Heilkunst.*
By Arnold Sack. *Julius Springer*
4.50 marks *Berlin*
5½ x 8½; 87 (paper)

A selection of quotations from the writings of Hippocrates, translated into German and assembled under 29 heads. The choice of material is excellent. While primarily intended for medical students, the general biologist will find much of interest in the book, and except in such a form he is not likely to read Hippocrates at all.

LIVING CREATURES. *Studies of Animal and Plant Life.*
By C. von Wyss. *A. and C. Black, Ltd.*
12s. 6d. net *London*
5½ x 8½; xi + 406

An excellent "nature study" book, by a successful teacher of "Natural History in the wide sense." There are 27 chapters, of which 21 deal with common animal forms, chiefly insects, while the remaining chapters are devoted to plant topics. The book is well written; and, as Prof. J. Arthur Thomson says in his Foreword, "gives us glimpses of the Drama of Life." There is an index.

EXPERIMENTAL EMBRYOLOGY.
By Thomas H. Morgan.
Columbia University Press
$7.50 5⅞ x 9⅛; xi + 766 *New York*

In a later number of THE QUARTERLY REVIEW OF BIOLOGY this important volume will receive extended notice.

HUMAN BIOLOGY

SYMBOLISM. *Its Meaning and Effect. By Alfred North Whitehead.*
The Macmillan Co.
$1.50 5 x 7⅝; x + 88 *New York*

This small volume includes three lectures given at the University of Virginia, under the Barbour-Page Foundation. At the start we are given this definition:

> The human mind is functioning symbolically when some components of its experience elicit consciousness, beliefs, emotions, and usages, respecting other components of its experience. The former set of components are the "symbols" and the latter set constitute the "meaning" of the symbols. The organic functioning whereby there is transition from the symbol to the meaning will be called "symbolic reference."

The author then develops the significance and consequences, philosophical and social, of this kind of mental activity.

> It is the first step in sociological wisdom, to recognize that the major advances in civilization are processes which all but wreck the societies in which they occur:—like unto an arrow in the hand of a child. The art of free society consists first in the maintenance of the symbolic code; and secondly in fearlessness of revision, to secure that the code serves those purposes which satisfy an enlightened reason. Those societies which cannot combine reverence to their symbols with freedom of revision, must ultimately decay either from anarchy, or from the slow atrophy of a life stifled by useless shadows.

ENVIRONMENT AND RACE. *A Study of the Evolution, Migration, Settlement and Status of the Races of Man. By Griffith Taylor. Oxford University Press*
$7.50 5½ x 8½; xv + 354 *New York*

This is a study of the population problem along anthropological lines, by the head of the Department of Geography in the University of Sydney. The book starts with the thesis that "the world problem of today is the adjustment of the nations to the crowding which for the first time in history is affecting the whole earth." The discussion of this, and various subsidiary problems which arise from it, is divided into four parts. The first is introductory, stating the problem and the technique to be used in its discussion. The second part deals with "The Changing Environment and Race Distribution," in the past. It is a comprehensive review of the author's views as to the forces which have influenced migration. The third part is devoted to a discussion of the white race in the Australian environment at the present time. Finally, the fourth part of the book is given to a prophesy as to the future distribution of the white race. The conclusion reached is embodied in the following table:

Future white settlement and its political control

	BRITISH	U. S. A.	OTHER STATES	TOTAL
	millions	*millions*	*millions*	*millions*
I. North American region (52 per cent of total) ...	179	513	10	702
II. European region (29 per cent of total).....	60	...	326	386
III. Argentine region (8.5 per cent of total).....	...	...	115	115
IV. South African region (6 per cent of total).....	76	...	6	82
V. Australian region (4.5 per cent of total)	62	...	...	62
Total.....	377	513	457	1,347
Percentage.....	28	39	33	100

Whether one agrees with all the author's conclusions or not this is an extremely interesting and provocative book.

ORGANIC INHERITANCE IN MAN.
By F. A. E. Crew. *Oliver and Boyd*
12s. 6d. *Edinburgh*
$5\frac{1}{2}$ x $8\frac{3}{4}$; xxviii + 214

This volume embodies the subject matter of a series of lectures to the medical profession of Birmingham, given by the distinguished Director of the Animal Breeding Research Department of the University of Edinburgh, as the first course under the William Withering Memorial. In the publication of the lectures the author has deemed it reasonable "to avoid any strenuous effect to observe meticulous accuracy and elaborate detail, but rather to attempt to give an intelligible presentation of principle. Authorities, though abundantly quoted, are not named, and there is no bibliography."

Professor Crew presents in this volume one of the best accounts that we have ever seen, for the intelligent reader not specially trained in biology, of the basic principles of genetics, on the one hand, and of the known facts of human inheritance, on the other hand. Being at once a master in the field of genetics and a medical man, he is peculiarly fitted for such a task. The last chapter of the book is entitled "Concerning the Implications of Genetic Fact and Theory." In its eight pages is embodied a splendid statement of a sound eugenic position, with a minimum of the preaching usually found in eugenical writings. We like particularly the following paragraph:

> But who shall sit in judgment and separate fit from unfit? These are relative terms, and in their definition one must allow for differences in point of view. Before action is taken, it is essential that man shall know what is man and what man may become. If and when it is decided what kind of thing mankind shall become, if and when standards of merit have been constructed, then the biologist will be able to help in the achievement of these by indicating the most promising methods of approach. But the biologist alone is not competent to draw up these standards: neither is the enthusiastic amateur statesman whose only claim to note is his sincerity.

An appendix carries some 50 odd pedigree charts showing the familial incidence and mode of inheritance of various human characteristics, particularly diseases.

HUMAN STERILIZATION.
By Rev. John A. Ryan.
National Catholic Welfare Conference
Washington, D. C.
$5\frac{3}{8}$ x $8\frac{1}{4}$; 10 (paper)

Father Ryan, who is an acute person, starts by quoting from André Siegfried's *America Comes of Age*, and then says:

> Once men reject the truth that the human person is intrinsically sacred, that even his body should be treated with reverence, they can easily persuade themselves that any person may be used in any fashion for the benefit of society. The difference between the social inconveniences arising from the existence of too many imbeciles and that resulting from the presence of too many Negroes, Mexicans or other non-Nordics, is a difference only of degree—possibly in favor of the imbeciles. If sterilization is no degradation of personality, no violation of natural rights, why should it not be applied to all the inferior classes that bring more inconvenience than convenience to the politically dominant *élite*?

The question seems to us a hard one to answer, but then rhetorical questions often are difficult to deal with adequately. In fact that seems to be one of the main reasons why people ask them.

Dr. H. H. Laughlin's "model eugenical sterilization law" is discussed, and it is pointed out that in that potential statute a "socially inadequate person" is defined as one who, along with other sad stigmata, "fails chronically in comparison with normal persons to maintain himself or herself as a useful member of the organized social life of the State."

We agree with Father Ryan that this is

a bit too inclusive. Furthermore it seems prolix. Why not define a socially inadequate person as one who "is disapproved of by Mr. A, or Mr. B, or Mr. C?" Or, if anyone of these, being a modest man, dislikes the publicity this would involve, substitute for his name that of the Hot Water Haven and World Eugenic Society, or the Ku Klux Klan, or the Anti-Saloon League? They all labor for noble causes and dislike objectionable people.

THE BUILDERS OF AMERICA.
By Ellsworth Huntington and Leon F. Whitney. *William Morrow and Co.*
$3.50 5¾ x 8¾; xiv + 368 *New York*

A contribution to eugenic evangelism dedicated to Irving Fisher, and ending on the following high note:

> Positive eugenics will increase the rarer, lovelier blossoms in the Queen's garden, and improve the commoner ones. It will restore to the garden the borders and beds of beautiful pansies like unto the black velvet gown of a bishop, the yellow silk of a duchess, the royal purple of a king, the motley of the gayest of clowns, and the white robe of a bride. It will do far more than this, for when the Queen's garden has enough seed of these rare kinds, and when sufficient seed is carefully preserved, lo, here and there, and then all over the broad land even the little flower beds of the peasants will be bright with blossoms like those in the Queen's own garden.

The book contains a large amount of interesting statistical material, some of which is new, bearing directly or indirectly upon eugenic problems.

PRIMITIVE MAN. *His Essential Quest. By John Murphy.* *Oxford University Press*
$5.00 5½ x 9; xiv + 341 *New York*

This is a comprehensive and intelligent attempt to discuss the psychological evolution of human kind, and to evaluate the significance of mind as a factor in evolution in general. The point of view of the whole study is indicated by the following quotation:

> The process of integration through differentiation, which is the method of the creative evolution of the universe, takes conscious form in man. It expresses itself in man's essential quest, which is directed towards the unification of his life. In this quest for unity within himself, he is seeking always a deeper and more sensitive integration, together with the utmost possible variety of differentiation. The imperfection of the instruments with which he works at the earlier stages of his human evolution—in particular, his imperfectly coördinated brain and mind—accounts for the imperfection of his earlier attempted unifications, and the manifold forms of his theories and customs. The integration of man's inner life involves certain integrations of his environment, of his world, including his fellows and his societies, unifications of himself with his world and of his world with himself.

There is a brief, but well chosen bibliography.

A SHORT HISTORY OF WOMEN.
By John Langdon-Davies. *The Viking Press*
$3.00 5¾ x 8¼; xiv + 382 *New York*

A most interesting book, which has been in the "best seller" class. The central thesis of the book, supported by much entertaining material derived from anthropological literature and the author's own observations, is that the history of women is the

> history of human ideas about the nature and differences of the two sexes; and as we have followed it, these ideas have consistently been based upon the same mistaken notions about biology. The primitive savage, the primitive Christian, the feudal knight, the seventeenth-century Puritan, the eighteenth-century essayist, the Victorian drawing-room tea-drinker; all alike thought and acted about women as they did because the same superstitions about biology and the same misinterpretation of feelings were common to all. The dawn came when people began to suggest that women were quite as

reasonable by nature as men, and that wrong education was responsible for any difference between them in this respect. After that came political emancipation and economic emancipation, until today we can say that the first is complete and the second almost as far advanced as it is for individuals of the male sex.

Not being a pedant or a professor the author is not afraid to write with some wit and humor.

THE MEINI HIRION AND SARNS OF ANGLESEY (*Considered in relation to the early Hundred System*). *A Key to the Antiquities of Britain.*
By William Evans *William Evans*
2s. 9d.
Pen-y-Bont, Red Wharf Bay, Anglesey
5¼ x 8¼; 49

"Meini Hirion" are menhirs. This book is a concise account of an investigation which must have cost the author a great deal of time and labor. The conclusion is that these stone monuments were boundary stones marking roads which divided the island into blocks of sixteen square miles each. Each square mile is supposed to be a township. Giraldus Cambrensis, who lived while the ancient "Hundred System" was still followed in Wales, says that Anglesey was divided into three Hundreds, made up of 343 townships or *trefydd*. There are in fact 343 plots of one square mile each on the island after allowing for roads and public spaces. There is thus evidence in favor of Mr. Evans' theory.

SOCIALITY. *The Art of Living Together.*
By Atkinson Lee. *Holburn Publishing House*
5 shillings 5 x 7½; xxvi + 305 *London*

This book is more in the tone of a somewhat pallid Unitarian tract than a scientific treatise. The general idea is that social living is not "either a science or a duty, but an act." The attempt is made to measure social values in terms of aesthetics. It is held that only in the religious realm can full sociality be realized. The book abounds in beautifully turned phrases, and should prove a veritable boon to parsons hard up for sermon material. The biologist will find it less useful.

THE NATURAL HISTORY OF A SAVANT.
By Charles Richet. Translated from the French by Sir Oliver Lodge. *George H. Doran Co.*
$2.00 net 5 x 7½; xi + 155 *New York*

This translation of a most entertaining book, which every scientific man should read, and particularly the beginner in science, is extremely well done. It preserves well the charm of the original. The natural history of great men is a branch of human biology too much neglected. While Richet's little book was written primarily for fun, both his and the reader's, it contains much real wisdom, and some brief sketches of really great men, which in their delicacy and sharpness of detail remind one of the engravings of the Little Masters.

THE RACIAL CHARACTERS OF THE SWEDISH NATION.
Edited by H. Lundborg and F. J. Linders.
The Swedish State Institute for Race Biology
100 Swedish crowns *Uppsala*
(*American distributor G. E. Stechert and Co., N. Y.*)
11¼ x 15; xiv + 108 + 44 plates
(paper)

A magnificent contribution to physical anthropology and eugenics, the result of

coöperative effort, ably guided by the distinguished Director of the *Swedish State Institute for Race Biology*. Following a brief historical section comes the first part of the main work, which includes seven chapters on the general anthropology and demography of the Swedish people. The second and largest section of the work is devoted to the exhibition and analysis of extensive series of anthropometric measurements. The final main section is devoted to the results of certain special investigations, bearing upon the main theme. At the end are 44 plates of beautifully reproduced photographs of Swedish types. No student of human biology can do without this book.

THE SURVIVAL OF THE UNFITTEST. *By Charles Wicksteed Armstrong.*

The C. W. Daniel Co.

6 shillings net $4\frac{3}{4}$ x $7\frac{1}{4}$; 160 *London*

An entertaining and forceful contribution to eugenic discussion. The book presents arguments in opposition to about all forms of social uplift—particularly organized charity—except eugenics and, by inference, birth control. Eugenic doctrines are presented as the solution of most of our troubles, and in one chapter, called "A Fascinating Scheme," a plan for a Eugenic Settlement is worked out in detail.

HUMAN ENVIRONMENT AND PROGRESS. *The Outline of World Historical Geography.* *By W. R. Kermack.*

W. and A. K. Johnston

4 shillings *Edinburgh*

$4\frac{7}{8}$ x $7\frac{1}{4}$; viii + 231

This little book is developed in three sections. The first lays down the principles of historical geography, which amounts to human ecology historically treated. The second section, which comprises somewhat more than half the book, deals with the British Empire and the United States. The final section is devoted to the rest of the world. The treatment is highly condensed. Perhaps partly because of the condensation, there are some careless slips in details. But on the whole it is a readable, interesting, and informative book, well illustrated, but unfortunately lacking an index.

THE EARLY HISTORY OF MAN. *With Special Reference to the Cap-Blanc Skeleton. Anthropology Leaflet 26.* *By Henry Field.*

Field Museum of Natural History

25 cents $5\frac{1}{2}$ x $8\frac{1}{2}$; 15 + 8 plates *Chicago*

The rock sculpture at Cap Blanc, near Moustier, is one of the great sights of the world. Few things can give the person, sufficiently intelligent to grasp its significance as a document in the history of human kind, a greater thrill than this frieze of horses, sculptured in high relief on the cliff face, with an artistry that has rarely been equalled. The little booklet from the Field Museum tells the story of this prehistoric station briefly, but extremely well, and with adequate illustrations.

ANCIENT CIVILIZATIONS. *From the Earliest Times to the Birth of Christ.* *By Donald A. Mackenzie.*

Blackie and Son, Ltd.

12s. 6d. $5\frac{3}{8}$ x $8\frac{1}{4}$; xix + 283 *London*

This volume deals with the ancient empires of Egypt, Asia, and Southeastern Europe from the earliest times of which

there is record down to the birth of Christ. Special attention is given to origins and to attempts to connect history with prehistory. The book is abundantly illustrated with excellent photographs, and will be found useful to the reader who wishes to get, in brief space, a reasonable knowledge of the beginnings of human history.

HEALTHY GROWTH. *A Study of the Relation Between the Mental and Physical Development of Adolescent Boys in a Public Day School.*
By Alfred A. Mumford.
Oxford University Press
$5.00 *New York*
5⅜ x 8¼; xxiii + 348

A well-written account of the growth and physiology of English schoolboys. Substantially all the thorough, careful observations made point towards the establishment of a positive relationship between mental and physical growth. Scholars, compared with non-scholars, are superior in respect of the condition of the mucous membrane of nose and throat; they have better vision, and teeth with less tendency to decay. The book is packed with interesting observations and is an important contribution to the literature of child hygiene and public health in general, as well as to physical anthropology.

FIGHTERS OF FATE. *A Story of Men and Women Who Have Achieved Greatly Despite the Handicaps of the Great White Plague.*
By J. Arthur Myers.
The Williams & Wilkins Co.
$3.00 5⅛ x 7½; xix + 318 *Baltimore*

Brief biographies of 23 men and one woman who had, or have, tuberculosis and have attained fame, in greater or less degree, by their achievements in one or another field of human endeavor. The sketches are entertainingly written, and the whole forms an interesting contribution to the literature of human biology. Dr. Charles H. Mayo contributes an introduction. The book is beautifully printed and bound.

IMMIGRATION CROSSROADS.
By Constantine Panunzio.
The Macmillan Co.
$2.50 5¼ x 7⅜; ix + 307 *New York*

A welcome addition to the literature of immigration. The author brings cogent, penetrating, and well deserved criticism of the existing immigration law of this country. He pleads for a consideration of the whole subject from an international point of view, and for a selection of immigrants based upon sound tests of individual worth, rather than the indiscriminating and ruthless exclusion of good and bad alike, if they happen not to be Nordics.

DIE GRUNDLAGEN DER CHINESISCHEN EHE. *Eine historisch-ethnographische Studie auf Grund des Gesetzbuchs der T'ang-Dynastie und Mandschu-Dynastie sowie ausgewählter klassischer und philosophischer Literatur.*
By Erich Schmitt. *F. A. Brockhaus*
14 marks 6 x 9; 223 (paper) *Leipzig*

An interesting and valuable contribution to the literature of human biology. The author, who is *Privatdozent* in the University of Berlin, has combed the classical, philosophical, and legal literature of China for material regarding marriage. The book is thoroughly documented, and

will serve as a useful reference source for occidental students.

DATEN UND TABELLEN FÜR DEN PRAKTIKER.
By H. von Hoesslin. *Georg Thieme*
3.25 marks 4 x 6¾; 98 (paper) *Leipzig*

A useful little compilation of numerical data of interest primarily to medical men, but also to physiologists, anatomists, and students of human biology generally. The range of facts presented is wide. Every biologist will find this volume worth a great deal more than it costs as a handy reference source.

IMMIGRATION RESTRICTION. *A Study of the Opposition to and Regulation of Immigration into the United States.*
By Roy L. Garis. *The Macmillan Co.*
$4.00 5½ x 8½; xv + 376 *New York*

A heavily documented review of the immigration legislation of the United States, which will be useful as a reference work. The book is introduced by a Foreword by Mr. Albert Johnson, chairman of the House committee on immigration and naturalization.

GUIDE TO PHYSICAL ANTHROPOMETRY AND ANTHROPOSCOPY.
By Chas. B. Davenport.
Eugenics Research Assoc.
75 cents *Cold Spring Harbor, N. Y.*
4 x 6¾; 53

A useful little handbook of instruction in anthropometric technique, primarily intended for the eugenic field worker. It constitutes the first number of a series contemplated by the Eugenics Research Association.

ZOOLOGY

DE LINNÉ À JUSSIEU: *Méthodes de la Classification et Idée de Série en Botanique et en Zoologie (1740–1790).*
By Henri Daudin. *Félix Alcan*
25 francs *Paris*
5½ x 8⅞; ii + 264 (paper)

CUVIER ET LAMARCK: *Les Classes Zoologiques et l'Idée de Série Animale (1790–1830).*
By Henri Daudin. *Félix Alcan*
60 francs *Paris*
5½ x 8⅞; Vol. I, xiii + 460 (paper)
Vol. II, 338 (paper)

The history of the theory and practice of taxonomic classification is, in a very considerable sense, the history of zoology as a whole. These three volumes by Dr. Daudin can only be regarded as a masterly accomplishment of an extremely difficult task. They constitute a contribution of first importance to the literature of the history of science.

Because of the magnitude and difficulty of the task the author has wisely set certain limitations upon his work. The first and most important is that he leaves to one side the question of genera and species and confines his attention to phyla. He shows how the supposedly continuous series—the *Scala naturae*—which was in the mind of the earlier taxonomists, came to be replaced by the great independent natural groups which today we regard as constituting the animal kingdom.

Another limitation is that, in the later period, he confines his attention largely to the French work. This however is justified because in the period of which he was writing France was the center of the zoological world. Cuvier and Lamarck were the great figures, with Etienne Geoffroy St. Hilaire, Latreille, Savigny, de Blainville, and Serres as the stars of lesser relative magnitude, but still of great absolute brightness.

The volumes are abundantly documented bibliographically.

BIRDS AND BEASTS OF THE GREEK ANTHOLOGY.

By Norman Douglas.

Obtainable from Norman Douglas, c/o T. Cook and Son,

$6.00 $5\frac{1}{2}$ x $8\frac{1}{2}$; 219 *Florence, Italy*

This delightful and charming volume, privately and beautifully printed in an edition of five hundred numbered and signed copies, is the kind of book to be written under conditions which can only fill with envy and longing the heart of the poor devil tied to a dingy laboratory on a raw March day. Let the author tell about it.

Books have been written on the Natural History of the Bible, on that of Shakespeare, of Homer, Virgil and so forth: why not a similar one on the fauna of the Greek Anthology—though the flora, perhaps would be even more interesting? So I often thought, while reading and re-reading this marvellous collection which has been my companion for many months past. Three years, I finally concluded, might suffice for the venture. Three years, under some vine-wreathed arbour, with the necessary books at one's elbow, and one's soul at ease. Such a thing, it is obvious, should be a holiday performance; written *con amore* and not otherwise; in reverential, playfully-erudite fashion. Three years or even more; for I soon realized that the enterprise might well blossom—why not?—into a general treatise on ancient Natural History and the changes in animal economy which have occurred in the interval between then and now; that it would open up, incidentally, a number of questions social, aesthetic, and humanitarian, showing how the attitude of mankind towards birds and beasts has altered since those days. Three years, I kept on saying to myself—where shall they be found?

I shall not find them.

Be that a pretext for putting together the following notes which may serve as material for some one more fortunately situated. The pencillings then scrawled in my Anthology are fast fading; I amplified them later with references to such authorities as were accessible, but a good many others would have to be consulted if the undertaking were to be brought up to date, such as, for instance, von der Mühle's book on the Birds of Greece, which I have not been able to procure.

An undertaking, for the rest, of the gentlemanly kind; quite useless.

So it is throughout, just utterly useless, perfectly delightful literary gossip about birds and beasts, good food, and such like things. Perhaps the most important thing in the volume is the author's recipe for cooking a *langouste*.

A NATURALIST AT THE DINNER TABLE.

By E. G. Boulenger.

Gerald Duckworth and Co., Ltd.

6 shillings 5 x $7\frac{1}{2}$; 160 *London*

A pleasantly and authoritatively written contribution to the ancillary literature of gastronomy. It is not a cookbook, but aims to inform the *bon vivant* about the natural history of many of the things which come to his plate. No epicure will fail to add this entertaining little volume to his library.

REALITIES OF BIRD LIFE. *Being Extracts from the Diaries of a Life-loving Naturalist.*

By Edmund Selous. Constable and Co., Ltd.

14 shillings *London*

$5\frac{1}{2}$ x $8\frac{3}{4}$; xvi + 351

A highly interesting contribution to natural history. It is a detailed record of field notes made in connection with "the intensive watching of birds in natural surroundings." A wide range of species is covered. Especial attention is given to courtship, mating, and nesting behavior. In the case of the ruff (*Pavoncella pugnax*) Mr. Selous' observations demonstrate sexual selection in the classic Darwinian

sense; the female, in three particular cases, having perfect freedom of choice among many suitors, chose exceptionally handsome and brilliant mates. Besides its value as a scientific record the book has great literary charm.

Professor Julian Huxley contributes an introduction.

THE BIOLOGY OF THE FROG.
By Samuel J. Holmes. *The Macmillan Co.*
$2.75 5 x 7⅜; ix + 386 *New York*

The fourth, thoroughly revised edition of a standard elementary text in zoology. The revision has been mainly in the physiological sections of the book.

ZOOLOGY OF COLORADO.
By Theodore D. A. Cockerell.
University of Colorado
$2.00 6 x 9; vii + 262 *Boulder*

A semi-popular systematic account of the fauna of Colorado, with the bulk of the space devoted to mammals, birds, and insects. The book should be extremely useful in aiding the non-professional person to identify the common animals of the region. It is one of the Semi-Centennial Publications of the University of Colorado.

THE FUR-TRADE OF CANADA.
By H. A. Innis.
University of Toronto Library
$2.00 6 x 9; 172 *Toronto*

This is the first of a projected series of studies of the principal industries of Canada, made under the aegis of the Department of Political Science of Toronto University. While primarily economic in its outlook, it contains a great deal of information of interest and value to the ecologist.

A CONTRIBUTION TO THE KNOWLEDGE OF TWENTY-ONE SPECIES OF THE GENUS UPOGEBIA LEACH.
By J. G. de Man. *Martin Nijhoff*
9 guilders *The Hague*
9⅞ x 12⅞; 58 + 6 plates (paper)

A detailed systematic account, with abundant illustrations, of the taxonomy of the genus *Upogebia*, decapod crustacea belonging to the *Thalassinidae*, or *Callianassidae*.

SOCIAL LIFE IN THE ANIMAL WORLD.
By Fr. Alverdes.
Harcourt, Brace and Co., Inc.
$3.75 5½ x 8½; ix + 216 *New York*

An attempt at a comprehensive survey of animal sociology, the original German edition of which has already been noticed in The Quarterly Review of Biology. The translation is excellent.

SCIENCE OF ANIMAL LIFE. *An Introduction to Zoölogy. Treating of Animals: Their Structure, Development, Reactions to Their Environment, and Relation to Man.* *By William M. Barrows.* *World Book Co.*
$1.76 *Yonkers-on-Hudson, N. Y.*
5⅛ x 7⅜; ix + 389

A comprehensive high school text book of zoology, well illustrated, and excellently organized for teaching purposes.

A HANDBOOK OF THE BIRDS OF EASTERN CHINA (*Chihli, Shantung, Kiangsu, Anhwei, Kiangsi, Chekiang, Fohkien, and Kwangtung Provinces*). Part IV (*Containing Families Ploceidæ, Fringillidæ, Bombycillidæ, and Hirundinidæ*).
By J. D. D. La Touche. *Taylor and Francis* 7s. 6d. *London*
6¼ x 9; 106 + 5 plates (paper)

Taxonomic, with notes on seasonal and geographic distribution, and, to a smaller extent, on habits.

BOTANY

UNTERSUCHUNGEN ÜBER DIE LICHTVERTEILUNG IN AVENA-KOLEOPTILEN UND ANDEREN PHOTOTROPISCH REIZBAREN PFLANZENORGANEN BEI EINSEITIGER BELEUCHTUNG.
Botanische Abhandlungen, Heft 12.
By Erich Nuernbergk. *Gustav Fischer* 19 marks *Jena*
6½ x 9½; 162 + 12 plates (paper)

A contribution to plant physiology of the first importance. The author has devised a method of measuring with physical precision the penetration of light into plant tissue. The principle of the method is that the cross-section (or longitudinal section) of an organ illuminated from a certain direction is photographed at right angles to this direction, and the photograph so obtained is subsequently photometrically registered and measured. Experiments were conducted with five forms that have been much used in studies of phototropism, namely the hypocotyls of *Helianthus* and of *Panicum maliaceum*, the hypocotyl and coleoptile of *Setaria italica*, the coleoptile of *Avena*, and the root tip of *Sinapis alba*. Space is not available to summarize all the interesting results. But the type of result obtained may be indicated by the fact that in the case of *Helianthus*, with concentrated illumination with white light on one side, the intensity of illumination is 4.6 times greater on the lighted than on the shaded side. There is selective absorption for different regions of the spectrum, being ⅔ for blue light if that for red light be taken as 1.

PLANT HUNTING
By Ernest H. Wilson. *The Stratford Co.*
$15.00 6¼ x 9½ *Boston*
Vol. I, xxix + 248 (paper)
Vol. II, ix + 276 (paper)

The author of these beautifully printed and superbly illustrated volumes is keeper of the Arnold Arboretum of Harvard University. He starts by saying that between 1899 and 1922 he "wandered about the world in search of plants." What an altogether delightful occupation!

> In these volumes I have attempted to give some account of the lands visited, of their discovery, their vegetation, and to tell in a general way also of the work done by early plant hunters. All parts of the world have added to the common store of garden material, but the countries sketched are among the richest sources of supply. Such a task as here attempted must, of course, be discursive since finality is obviously impossible. I have merely lifted a corner of the curtain so as to allow a peep at the general scene.

The result is a charming book, full of extraordinary interest, not only to the botanist but also to the general reader. The illustrations, of which there are 128 are a great feature of the work. They are mostly photographs of trees and the landscapes in which they occur. But they are superb photographs, of rare and beautiful trees. No gentleman's library should lack this book.

LES ÉQUISÉTINÉES DU QUÉBEC.
By Frère Marie-Victorin.
University of Montreal
$1.00 *Montreal*
6 x 9; xi + 137 (paper)

LES GYMNOSPERMES DU QUÉBEC.
By Frère Marie-Victorin.
University of Montreal
$1.00 *Montreal*
6 x 9; xii + 147 (paper)

SUR UN BOTRYCHIUM NOUVEAU DE LA FLORE AMÉRICAINE ET SES RAPPORTS AVEC LE B. LUNARIA ET LE B. SIMPLEX.
By Frère Marie-Victorin.
University of Montreal
50 cents *Montreal*
6 x 9; 22 + 3 plates (paper)

These papers constitute Nos. 9–11 of the contributions from the Botanical Laboratory of the University of Montreal. The first two are systematic floristic monographs, well arranged and carefully done, with good illustrations, dealing respectively with the horse-tails and the gymnosperms of Quebec. The third is a biometric study of three species of *Botrychium*, undertaken for the purpose of taxonomically distinguishing them.

PLANTS OF THE PAST. *A Popular Account of Fossil Plants.*
By Frank H. Knowlton.
Princeton University Press
$3.50 *Princeton, N. J.*
6 x 9; xix + 275

The author's purpose was to produce "a work of moderate size, written in non-technical language, that should set forth the salient facts regarding the plants that have clothed the earth from the time when life first appeared down to the present." This purpose has been excellently realized. The style is simple and straight-forward; the book is beautifully printed and illustrated; and the arrangement of the material is well calculated to sustain the interest of the general reader. We commend the book particularly to workers in other fields of science who wish to get a general idea of the present status of palaeobotany, without too much trouble.

COLORADO PLANT LIFE.
By Francis Ramaley. *University of Colorado*
$2.00 6 x 9; viii + 299 *Boulder*

This volume, in the series of Semi-Centennial Publications of the University of Colorado, is a highly successful attempt "to present in simple form some of the larger facts of plant life for the man or woman who is not trained in botany but who wishes to gain an appreciation of nature. Care has been taken to make all statements accurate, and it is hoped that the book will not seem shallow just because it is non-technical." Well illustrated, charmingly written, and sufficiently documented and indexed, the book can be highly recommended to the general reader and to the worker in other branches of science who wants to know something of the vegetation which clothes the earth about him.

ROOT DEVELOPMENT OF VEGETABLE CROPS.
By John E. Weaver and William E. Bruner.
McGraw-Hill Book Co.
$4.00 5¾ x 9; xiii + 351 *New York*

This is a companion volume to Weaver's *Root Development of Field Crops*, already noticed in these columns, and is largely based upon the authors' own investigations. Thirty-three separate chapters

are devoted to descriptions, mostly with original illustrations, of the root system of as many different garden vegetables. There is a bibliography of 182 titles, and an index. The book is an important contribution to the literature of ecology, as well as to that of horticulture and agriculture.

LA VIE DE LA CELLULE VÉGÉTALE.
By Raoul Combes. *Armand Colin*
9 francs $4\frac{1}{4}$ x $6\frac{5}{8}$; 216 (paper) *Paris*

This excellent little treatise, which puts its emphasis mainly upon the functional aspects of plant cytology, discusses in detail the following subjects: The morphological constitution, origin and physiological rôle of the protoplasm of the plant cell; the chemical constitution of protoplasm; the form, origin, physiological function, and chemical constitution of the nucleus; general characters of plastids and mitochondria; the amyloplasts, chloroplasts, chromoplasts, oleoplasts, and proteoplasts. There is a bibliography covering nine pages.

PLANT RESPIRATION.
By S. Kostychev. Translated and Edited by Charles J. Lyon.
P. Blakiston's Son and Co.
$2.50 6 x 9; xi + 163 *Philadelphia*

Professor Lyon has done a real service to American students of plant physiology by providing this translation of Kostychev's treatise on respiration. It gives, as the translator says, a balanced, authoritative discussion of a subject which has made great advances in the twentieth century. The book is abundantly documented with citations of literature and will serve as a valuable reference work.

A LABORATORY MANUAL FOR THE STUDY OF GENERAL BOTANY.
By William E. Lawrence. *State College Press*
$1.80 6 x 9; 220 (paper) *Corvallis*

The third edition of a laboratory manual for a course in elementary botany, by the Associate Professor of Plant Ecology at the Oregon State College, based upon the idea that the "laboratory should be a place for study and investigation rather than merely an art or copy class. It should be a place where independent observations may be made and not a mere routine to be done for a grade."

THE ELEMENTS OF VEGETABLE HISTOLOGY.
By C. W. Ballard.
John Wiley and Sons, Inc.
$3.25 $5\frac{1}{4}$ x 8; xviii + 289 *New York*

The second edition, revised and enlarged, of a standard text, primarily intended for beginning students of pharmacy. The section on chemical reactions of plant tissues in particular has been enlarged. There is a brief bibliography of textbooks for reference use, and a detailed index.

THE STRUCTURE AND DEVELOPMENT OF THE FUNGI.
By H. C. I. Gwynne-Vaughan and B. Barnes.
The Macmillan Co.
$4.25 $5\frac{1}{2}$ x $8\frac{1}{2}$; xvi + 384 *New York*

A systematic review, extensively illustrated, of the biology of fungi, with the principal emphasis on morphology but without neglecting the physiological side. There is an excellent section on mycological technique and a bibliography covering 28 pages of fine print. The book is a valuable contribution to botanical literature.

AN ELEMENTARY LABORATORY GUIDE IN GENERAL BACTERIOLOGY. *By Harold J. Conn.*

The Williams & Wilkins Co.

$4.00 6 x 9; ix + 165 *Baltimore*

A combined laboratory guide and notebook for elementary classes in general bacteriology, designed to accompany the Conns' textbook *Bacteriology*.

DICTIONARY OF BACTERIOLOGICAL EQUIVALENTS. *French-English. German-English. Italian-English. Spanish-English.*

By William Partridge.

The Williams & Wilkins Co.

$4.00 $4\frac{7}{8}$ x $7\frac{1}{4}$; xi + 141 *Baltimore*

A brief but adequate dictionary of the equivalent English terms for French, German, Italian, and Spanish technical words used in writings about bacteriology.

DAS MIKROSKOP *und seine Benutzung bei pflanzenanatomischen Untersuchungen. Erste Einführung in die mikroskopische Technik, zugleich eine Erläuterung zu den Pflanzenanatomischen Tafeln von Niemann und Sternstein. By G. Niemann.*

Creutz'sche Verlagsbuchhandlung

2.20 marks *Magdeburg*

$5\frac{1}{2}$ x $8\frac{7}{8}$; 104 (paper)

The third edition of a laboratory manual for the elementary study of the microscopic anatomy of plants.

MORPHOLOGY

CONTRIBUTIONS TO EMBRYOLOGY. *Vol. XIX, Nos. 98 to 108 (Publication No. 380). No. 98. The Menstrual Cycle of the Monkey, Macacus rhesus: Observations on Normal Animals, the Effects of Removal of the Ovaries and the Effects of Injections of Ovaries and Placental Extracts into the Spayed Animals, by Edgar Allen. No. 99. Embryology of the Neuromuscular Spindle, by Fidel Cuajunco. No. 100. Development of the Mesoblast and Notochord in Pig Embryos, by George L. Streeter. No. 101. Growth of the Human Foot and its Evolutionary Significance, by William L. Straus, Jr. No. 102. Lymphatics of the Fallopian Tube of the Sow, by Dorothy H. Andersen. No. 103. Correlated Physiological and Morphological Studies on the Development of Electrically Responsive Areas in the Cerebral Cortex of the Opossum, by Orthello R. Langworthy. No. 104. Histological Development of Cerebral Motor Areas in Young Kittens Correlated with their Physiological Reaction to Electrical Stimulation, by Orthello R. Langworthy. No. 105. On the Placentation of the Tridactyl Sloth, Bradypus griseus, with a Description of some Characters of the Fetus, by George B. Wislocki. No. 106. A Study of the Implantation of the Ovum of the Pig from the Stage of the Bilaminar Blastocyst to the Completion of the Fetal Membranes, by Chester H. Heuser. No. 107. Development of the Human Heart From its First Appearance to the Stage Found in Embryos of 20 Paired Somites, by Carl L. Davis. No. 108. Observations on the Ovary of the Opossum, Didelphis virginiana, by Carl G. Hartman.*

Carnegie Institution of Washington

$6.25 paper binding *Washington, D.C.*

$7.25 cloth binding

$9\frac{1}{4}$ x $11\frac{1}{2}$; 300

The papers in this superbly printed and illustrated volume are of such extraordinarily even and high quality that it is difficult to pick out any one for special mention without seeming to be unfair to the others, and lack of space makes it impossible to review them all. Several of them break new ground, and some of them, notably Davis's paper on the

development of the human heart, are certainly destined to become classics of anatomical reference.

GOETHE'S MORPHOLOGISCHE ARBEITEN *und die Neuere Forschung.*
By Valentin Haecker. *Gustav Fischer*
5 marks 6½ x 9½; vi + 98 (paper) *Jena*

An expansion of lecture material, which gives a better conception of the significance of Goethe's biological ideas in relation to the modern viewpoint than anything which has hitherto appeared. The topics discussed are: History of Goethe's botanical studies; The intermaxillary. First emergence of the idea of type; The vertebral theory of the skull; The osteological type; Goethe as physiologist; "Urpflanze" and metamorphosis of plants; Goethe's ideas regarding the developmental mechanics of plants; The spiral tendency of plants; Goethe as predecessor of Darwin. Altogether this brochure is a useful contribution to the history of science.

RECENT ADVANCES IN ANATOMY.
By H. Woollard. *P. Blakiston's Son and Co.*
$3.50 *Philadelphia*
5¼ x 8; vii + 302

This little book maintains well the high standard of the "Recent Advances" series, other numbers of which have been noticed in these columns. The topics treated, in a readable and interesting fashion, are: Microdissection; tissue culture; oestrus, ovulation and menstruation; the youngest human ovum—the Miller ovum; growth centers and organisers; the morphogenesis of nerve fibres; vital staining; the origin of the cells of the blood; the cerebrospinal fluid; postural organs; the red nucleus; the extra-pyramidal system; the cerebellum; the projection of the retina in the central nervous system; protopathic and epicritic sensation; X-ray anatomy.

ÜBER DIE BESTIMMUNG DES ALTERS VON ORGANVERÄNDERUNGEN BEI MENSCH UND TIER AUF GRUND HISTOLOGISCHER MERKMALE. *Mit besonderer Berücksichtigung der Hämosiderinbildung bei Pferd, Rind und Hund.*
By Curt Krause. *Gustav Fischer*
6 marks 6½ x 9½; 120 (paper) *Jena*

A detailed account of an investigation of the time changes in pathological lesions, particularly those of an inflammatory character. The experiments were made on horses, cattle and dogs. There are extensive bibliographies following each section of the work.

EXTREMITÄTENENTWICKLUNG UND POLYDACTYLIE BEIM PFERDE. *Die Ontogenese des Hand- und Fussskelets, Varianten am Carpus und die Beurteilung der "entwicklungsbedingten" Polydactylie bei Equus caballus. Zoologische Bausteine. Band 1, Heft 3.*
By Fritz Drahn. *Gebrüder Borntraeger*
16 marks *Berlin*
6½ x 10; viii + 206 (paper)

A comprehensive morphological study, based upon a rich material, of polydactyly in the horse, prefaced by a detailed study of the normal ontogeny of the skeleton of the fore and hind feet. There is a bibliography of 77 titles, but no index.

PHYSIOLOGY

NOXIOUS GASES *and the Principles of Respiration Influencing Their Action. By Yandell Henderson and Howard W. Haggard.* *The Chemical Catalog Co., Inc.*
$4.50 6 x 9; 220 *New York*

Professor Yandell Henderson is the leading American investigator of the physiological effects of poisonous gases. He and his colleague, Dr. Haggard, have performed a useful service in concisely summarizing in this volume the present state of knowledge in this field. They classify noxious gases and vapors into three main groups, viz., asphyxiants, irritant gases, and volatile drugs and drug-like substances. Following a general introductory chapter, three chapters are devoted to a clear and concise account of the physiology of respiration. After a detailed treatment of the various noxious gases and vapors, the book ends with a chapter on prevention and treatment of poisoning by such substances. Each chapter is followed by a brief, but well chosen, list of references to the literature. The book is well indexed.

MUSCULAR MOVEMENT IN MAN: THE FACTORS GOVERNING SPEED AND RECOVERY FROM FATIGUE. *By A. V. Hill.* *McGraw-Hill Book Co.*
$2.50 6 x 9; 104 *New York*

This book records the results of the experiments on the physiology of athletes which the author made while holding the George F. Baker lectureship in chemistry at Cornell University last year. The general point of view is that of an engineering analysis of the work done by the human body, and an attempt at a rational explanation of how this work is done in terms of the physics and chemistry of the living substance. Professor Hill's work may truly be said to mark the initial development of a new era in human physiology.

LE SYSTÈME VEINEUX NORMAL ET PATHOLOGIQUE. *Guide des Malades et des Prédisposés. Varices—Phlébites—Hémorroides—etc.*
By Drs. Hugel and G. Delater.
Gaston Doin et Cie
15 francs $4\frac{1}{2}$ x 7; 182 (paper) *Paris*

This is supposed to be a guide for those who have or expect to have diseases of the venous system. The project is in many ways a curious one, and it is questionable whether there are many patients who would benefit by being handed such a book—even if it were written so simply that they could understand it all. Unfortunately, the authors seem to have kept in mind a medical audience as well as a lay one, and as a result they will probably "weary the unlearned, who need not know so much, and trouble the learned, who know it already." One wonders just what relation, if any, the writers bear to those who are selling the waters of Bagnoles. The section on therapeutics contains many exhortations to drink more of this particular fluid.

ÜBUNGEN AUS DER VERGLEICHENDEN PHYSIOLOGIE. *Atmung. Verdauung. Blut. Stoffwechsel. Kreislauf. Nervenmuskelsystem.*
By Hermann J. Jordan and G. Chr. Hirsch.
Julius Springer
19.50 marks *Berlin*
$6\frac{3}{8}$ x $9\frac{1}{2}$; viii + 272 (paper)

A very thorough and well worked out set of laboratory directions for a course in comparative physiology including both

vertebrates and invertebrates, covering the topics of respiration, digestion and metabolism, the blood and its circulation, and the nerve-muscle system. The directions for practical work are accompanied by explanatory text material. The whole presents the material for an extremely well-rounded course. American teachers of biology will do well to look into this book.

DER MESKALINRAUSCH. *Seine Geschichte und Erscheinungsweise.*
By Kurt Beringer. *Julius Springer*
18 marks *Berlin*
6¾ x 10; v + 315 (paper)

This interesting volume reviews what is known about mescal, including its botany, chemistry and pharmacology, and then describes in detail an extensive experimental investigation of its physiological effects made by the author. More than a half of the book is devoted to detailed accounts of their introspective experiences by the persons who acted as subjects in the experiments. The book is a valuable contribution to the literature of physiology and psychiatry.

TIERPHYSIOLOGIE. *I. Stoffwechsel und Bewegung.*
By Konrad Herter. *Walter de Gruyter und Co.*
1.50 marks 4 x 6; 131 *Berlin*

A little handbook in the *Sammlung Göschen* on metabolism and movement, forming the first part of a treatise on animal physiology in this well-known series. It is intended primarily for high school teachers. The material is well chosen and presented in an interesting manner.

THE MENINGIOMAS *Arising from the Olfactory Groove and Their Removal by the Aid of Electro-Surgery.*
By Harvey Cushing. *Jackson, Wylie and Co.*
2s. 6d. 6⅛ x 9¾; 53 (paper) *Glasgow*

This is the Macewen Memorial Lecture delivered at the University of Edinburgh in 1927. The solid surgical meat is prefaced by eight pages of delightful historical gossip, with some good stories, about Macewen, the Hunters, and other medical worthies.

ANIMAL NUTRITION.
By T. B. Wood.
University Tutorial Press, Ltd.
3s. 6d. 4¾ x 7½; viii + 226 *London*

The second edition of a standard agricultural text by the distinguished professor of agriculture in the University of Cambridge. A few revisions of details constitute the only alterations from the first edition.

BIOCHEMISTRY

THE ANTISTERILITY VITAMINE FAT SOLUBLE E.
By Herbert McLean Evans and George O. Burr.
University of California Press
$5.00 10 x 13; 176 (paper) *Berkeley*

A monograph regarding the fifth definitely established vitamine. An account is here given of the work which the authors have done on the chemical purification of vitamine E. They conclude that: "There can be no doubt that there is a substance present in the active fractions which is specific for curing a specific type of sterility induced by certain purified diets. The cure has repeatedly been effected by as little as five milligrams

of the concentrated fractions fed on the day of positive mating. Controls have never given litters."

The topics discussed in this volume are:

General characterization of the sterility disease produced in rats by pure foods or other dietaries lacking fat soluble vitamine E; the histopathology of gestation in animals deprived of E; male sterility with dietaries lacking E; on the widespread occurrence of initial fertility in animals reared on simplified diets; distribution of vitamine E in foods of animal origin; distribution of the vitamine in foods of plant origin; proof of the existence of vitamine E in the tissues of animals reared upon natural foods and of its depletion in the tissues of animals reared upon synthetic rations; the survival of fertility in animals shifted from a diet possessing vitamine E to one deprived of it; the presence of vitamine E in the tissues of normal newborn young; proof of the use of vitamine E in the ordinary metabolic processes of the body; can an excess of vitamine E increase fertility beyond normal limits; the successful parental administration of vitamine E as a cure of sterility in female rats; the efficacy of a single curative dose of vitamine E administered at the beginning of gestation; determination of the minimal effective dose of vitamine E in the cure of sterility in the female rat; how late in gestation may we administer the vitamine to ensure the birth of living young; the solubility of the vitamine; stability of the vitamine; steps in the isolation and concentration of vitamine E.

This monograph is a worthy presentation of a fine piece of research.

LECTURES ON THE BIOLOGIC ASPECTS OF COLLOID AND PHYSIOLOGIC CHEMISTRY.

W. B. Saunders Company

$2.50 5⅜ x 7¾; 244 *Philadelphia*

There are six of these Mayo Foundation lectures, by the following persons, and on the indicated topics: Principles underlying colloid chemistry, by Robert A. Millikan; colloid chemistry in biology and medicine, by Martin H. Fischer; the physical properties of protoplasm, by Robert Chambers; adsorption and vital phenomena, by Ross A. Gortner; the physics of the ultramicroscope and optical properties of colloid particles, by E. Franklin Burton; the biological effects of light, by William T. Bovie.

This volume constitutes a useful popular introduction to the colloid field.

KURZES LEHRBUCH DER CHEMISCHEN PHYSIOLOGIE.

By Ernst Schmitz. *S. Karger*

16.80 marks *Berlin*

6½ x 9½; vii + 384

The second edition of a general reading text of physiological chemistry for medical students. There is abundant citation of the literature up to the middle of 1926. The chief relative value of the book, in comparison with others on the subject, is in its judicious and skillful condensation of the essentials in a broad and actively progressing field of biology.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 244. Aminieren und Amidieren.*

By Hans Sickel. *Urban und Schwarzenberg*

10 marks 7 x 10; 200 (paper) *Berlin*

Lieferung 248. Elektrodialyse, by Mona Spiegel-Adolf; *Die Methoden zur Bestimmung der Beweglichkeit und der Ladung kolloider Teilchen*, by Arne Tiselius; *Molekulargewichtsbestimmung der Eiweisskörper durch Zentrifugierung*, by Theodor Svedberg.

Urban und Schwarzenberg

7 marks 7 x 10; 125 (paper) *Berlin*

Lieferung 254. Chemische Reaktionen Organischer Körper im Ultravioletten Licht und im Licht der Sonne.

By Franz Bachér. *Urban und Schwarzenberg*

32 marks 7 x 10; 630 (paper) *Berlin*

These three numbers of the Abderhalden Handbook deal with various aspects of

biochemistry. The first is highly technical, and only of interest to the chemist. The second is of particular interest to the student of colloids. The third, while dealing with chemical technique, will be indispensable as a reference work for everyone studying the effect of light on organisms with any attempt at thoroughness.

SEX

WOMAN AND LOVE.

By Bernhard A. Bauer. *Boni and Liveright*

$10 $4\frac{3}{4}$ x $8\frac{3}{4}$; Vol. I, 353; Vol. II, xxvii + 396 *New York*

This is another one of those books whose sale is "strictly limited to members of the medical profession, psychoanalysts, scholars, and to such adults who may have a definite position in the field of psychology or social research." The line of those failing to qualify under this "restriction" will form at the left, if any. The "chosen problem" of the book is "the loving woman." In the 776 pages of these two volumes about everything is said upon this entertaining subject that well could be. Unfortunately for the scholarly use of the book it is not documented, though mainly consisting of a wide-ranging review of certain parts of the literature of anthropology, ethnology, sociology, and psychology, nor does it contain an index. There is, to be sure, a "Bibliography" which does not quite fill one page, and in which the references are not cited with exactness or completeness. For those who love to read about the sexual act in all its relations this book can be recommended.

BIOMETRY

FREQUENCY CURVES AND CORRELATION.

By W. Palin Elderton.

15 shillings $5\frac{1}{2}$ x $8\frac{3}{4}$; vii + 239 *Charles and Edwin Layton* *London*

This is a new and considerably enlarged and revised edition of the best textbook which has yet appeared for the student who wishes to learn the theory of Pearson's system of frequency curves. The chapters on correlation, contingency, probable errors, and goodness of fit have been rewritten and enlarged, and a new chapter on practical correlation has been added. An abridged course of reading is suggested to help those who are less interested in the mathematical side of the work and in the details of curve-fitting, but wish to know about the practical treatment of correlation, sampling, etc.

INTRODUCTION TO THE MATHEMATICS OF STATISTICS.

By Robert W. Burgess. *Houghton Mifflin Co.*

$2.50 $5\frac{3}{8}$ x $7\frac{3}{4}$; ix + 304 *Boston*

This volume accomplishes well the task implied in its title. It is intended to be of general usefulness to elementary students of statistics of all fields, and draws its examples from many of them.

PSYCHOLOGY AND BEHAVIOR

PHILOSOPHY.

By Bertrand Russell.

$3.00 $5\frac{1}{2}$ x $8\frac{3}{8}$; vi + 307 *W. W. Norton and Co., Inc.* *New York*

The considerable popular interest in philosophy which is a curious phenome-

non of these present times will be enhanced by this volume. Bertrand Russell is not only an outstanding philosopher in his own right, but he can write more cleverly and melodiously than any other present practitioner in the field of the higher mysteries. This book is first of all a searching critique of theories of knowledge, with special attention devoted to the implications in this direction of behaviorism. With much of the behavioristic position Russell agrees, but finally breaks with it fundamentally, on a metaphysical point. Having cleared the ground of older theories the author ends with an exposition of the healing virtues of his own eye water. It is a good book; worth buying and studying.

ZUR PSYCHOLOGIE DER TIERE UND MENSCHEN.

By W. Betz. *Johann Ambrosius Barth*
7.50 marks *Leipzig*

6 x 9¼; xi + 206 (paper)

A wide-ranging discussion of all sorts of human affairs and interests, in the light of comparative psychology. The author writes with vigor and dash, and the book in consequence makes interesting reading. We like his contribution to the eugenics problem, in which it is suggested that if only the most superior men were not, as a rule, so weak and uncertain sexually they could easily have some hundreds of children apiece, any stupid moral restrictions being really easily removable, and then there would be some hope of occasionally getting an individual as much above Gauss, Faraday, or Kant, for example, as they are above the ordinary university professor, while the average would be raised up to the level of these great men.

THE SIXTH SENSE. *A Physical Explanation of Clairvoyance, Telepathy, Hypnotism, Dreams and Other Phenomena Usually Considered Occult. Forty Years of Study, Observation and Experiment.*

By Joseph Sinel. *T. Werner Laurie, Ltd.*
6 shillings net *London*

4¾ x 7½; 180

This is an entertaining little book. The sense organ for "telepathic" and "clairvoyant" seeing is, according to Mr. Sinel, the pineal body. Children are more clairvoyant than adults because their pineal is bigger, and because the anterior fontanelle is not so tightly closed. Telepathy is the response of one brain to molecular vibrations in another. The simultaneous movements of a flock of starlings, for example, are taken as evidence of the occurrence of this phenomenon in animals. While it is very weak in spots, we think that most biologists will enjoy reading this volume. There is no law which compels anyone to agree with Mr. Sinel's theory.

THE MIND OF A GORILLA: PART II. MENTAL DEVELOPMENT. *Genetic Psychology Monographs, Vol. II, No. 6.*

By Robert M. Yerkes. *Clark University*
$2.00 *Worcester, Mass.*

6 x 9; 174 (paper)

This second report on the behavior of Congo, the young female gorilla brought from Africa by Mr. Ben Burbridge, maintains the high level of quality and interest set in the first report reviewed in an earlier number of THE QUARTERLY REVIEW OF BIOLOGY. In the year which intervened between the two studies Congo unquestionably developed mentally. Of particular interest in this volume is the account of the beginnings of her sex behavior.

LE DESSIN ENFANTIN.
By G. -H. Luquet. *Félix Alcan*
20 francs $4\frac{3}{4}$ x $7\frac{1}{2}$; 260 (paper) *Paris*

An interesting and scholarly discussion, with many illustrations, of children's drawings. The first half of the book deals with the psychological elements of children's drawings, and the last half with their evolution through successive stages. At the end a chapter is devoted to psychological and pedagogical conclusions.

THE MIND IN SLEEP.
By R. F. Fortune.
Kegan Paul, Trench, Trubner and Co., Ltd.
5s. $4\frac{3}{4}$ x $7\frac{1}{4}$; xii + 114 *London*

This little book derives its chief interest from the examples of dreams which it describes in detail. All of them are of the type of mental conflict dreams, and in the cases given the side that wins in the dream is the side that in working life is not in the ascendant. The theoretical discussion is highly technical and chiefly of interest to the psychiatrist.

DAS RECHNEN DER NATURVÖLKER.
By Ewald Fettweis. *B. G. Teubner*
5 marks 6 x $8\frac{3}{4}$; iv + 96 (paper) *Berlin*

An interesting digest of the anthropological literature regarding mathematical procedures among primitive peoples. The author finds a psychological phylogenetic parallelism to the ontogenetic development of the child in the highly cultured races, in respect to the evolution of mathematical thinking and technique. There is an extensive bibliography.

L'ESPRIT DE CONTRADICTION. *Ses Manifestations Individuelles et Collectives.*
By Paul Chavigny. *Marcel Rivière*
8 francs $4\frac{3}{4}$ x $7\frac{3}{8}$; 160 (paper) *Paris*

A psychological and sociological study of the cantankerous person, who is "agin" pretty much everything, individually and collectively. It is an entertaining and, in some degree, significant book. There is a short bibliography appended.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

RACIAL OLD-AGE. *Being Further Adventures in Philosophy and Containing an Exoneration of Woman.*
By Henry Allen *Henry Allen*
$1.00 6 x 9; 34 (paper) *Seattle*

This is an amusing book. The Foreword reads as follows:

> The manuscript for this booket was rejected by two New York publishing firms. No doubt their judgment was correct, especially so as to the prospects of future sales. However, being of a perverse nature, I have decided to publish it with my own labour, using for that purpose a multigraph machine. This is my second experience of this sort. My first, a booklet on gravitational theory, has a perfect "No sale" record. I am much consoled, however, for on visiting an important public library I found neither my own book, nor works of Sir Isaac Newton nor any of the notable writings of Captain T. J. J. See.

The central thesis is put this way:

> Applying philosophical principles to the problem, the author was enabled to develop the factors for determining racial old-age to the point where it may be possible easily to recognize its presence in the human races and individuals. The broad principle involved is: The race or specie, as it grows old, repeats the indications of senility to be found in the individual of the race or specie as he or she grows old. As a corollary: The causes of racial old-age are the same as those that bring about stoppage of

further advancement and hasten premature old-age and death in the individual of the race or specie. In other words the underlying thesis of this booklet is an antithesis to the principle that in the embryological development and even in infancy the individual repeats, to some extent, the evolutionary history of the race.

The development of this theme leads to many entertaining ideas. The temptation to quote is great but we have space for only one sample: "And who is to blame for this increasing feminization of modern western societies, following the course of ancient societies in that respect? . . . . Man is to blame. He is almost wholly to blame. The proof is very simple. Even in these degenerate days our average modern she-man possesses a greater degree of sensitiveness than the average modern he-woman."

JINGO.

By John Veiby. *John Veiby*
$1.00 *South Bend, Ind.*
5 x 7¼; 157 (paper)

The object of this book is "to create interest in a national religion." And it is *some* religion! The women's headquarters are to be called *Jingo Inns*, each with a wise old woman to whom the young girls tell their troubles and are advised as to how to get out of them. A feast of sorrow may be instituted, which would resemble that of the ancient women weeping for the lost Adonis. The headquarters for the men are to be called *Jingo Taverns*. They will be like the old-fashioned saloons—"pleasant places of rest and recreation." The Jingo Sabbath is to be on Saturday and is to be started by taking a bath, then putting on special garments, and going to bed. "What happens after this, we do not know, and should not know." But sleep will be one of the things. "There must be guardians around the precincts of Jingo during the observance of the Sabbath, whose duty it would be to keep away disturbers of the peace, and also to wake up or call to order those within, if they should be visited by evil dreams or a nightmare, in short, see to it that the observance goes on peacefully, free and happy."

We recommend Jingo to our readers. There are few ways known to us to get more fun for a dollar.

LE RETOUR ÉTERNEL ET LA PHILOSOPHIE DE LA PHYSIQUE.

By Abel Rey. *Ernest Flammarion*
12 francs 4¾ x 7½; 320 (paper) *Paris*

This volume, which appears in the *Bibliothèque de Philosophie scientifique*, is a detailed and scholarly discussion of the philosophical significance of modern thermodynamics and the kinetic theory of gases. The final position reached is that of Spinoza: "*Sentimus et experimur nos aeternos esse.*"

MEDICAL PALMISTRY *or The Hand in Health and Disease.*

By Katharine St. Hill. *Rider and Company*
7s. 6d. 6 x 9; ix + 132 *London*

This is the second volume of "The Book of the Hand." It is great stuff, considered as one more document to add to that large collection of treatises which evidence the odd ways in which the mind of *Homo sapiens* sometimes works. The authoress at the start enters a general disclaimer in this form: "apart from the hand I know but little of my subject." Every medical man who reads the book will agree. At the same time such a statement, which is reiterated on many pages of the book, does testify to real intellectual honesty. And

there is this further to be said that, after all, the lines of the hand are *a priori* no more inherently unpromising, considered as anatomical stigmata of constitutional anomalies, than are some of the characters seriously discussed in standard medical treatises on this subject.

EINSTELLUNG ZUR RÖNTGENOLOGIE. *Eine Untersuchung über die Einfügung der Röntgenstrahlenanwendung in Praxis, Forschung und Unterricht.*
By G. Holzknecht. *Julius Springer*
8.60 marks *Wien*
6 x 9; xii + 115 (paper)

One of the outstanding figures in roentgenology, a man who has watched the development of the speciality from its beginnings in 1895 to its enormous usefulness in 1926, feels the need for taking stock. The growth of the subject has been so rapid that there is much chaos and much need for finding out what is true and useful and what is not. He regrets that articles on the theory and practice of roentgenology are scattered through many books and journals where one would hardly expect to find them. They are written often from the points of view of many specialists who only incidentally are roentgenologists. The spread of interest in the subject is revealed also in the field of teaching, where it is hard to know what to do with students; should they get most of their knowledge of the roentgen ray in one department or should they pick it up here and there in the departments of physics, medicine, gastro-enterology, surgery, gynecology, urology, dermatology and orthopedics?

Similarly, what should be the training of the specializing roentgenologist? Should he ever be a layman? These and many other problems of great interest to American physicians are ably discussed. Unfortunately, Holzknecht's German may prove hard going for some.

CONTRIBUTION MÉTAPHYSIQUE *à la Méthode Expérimentale.*
By Louis Devos. *Georges Frère*
12.50 francs *Tourcoing*
6 x $9\frac{1}{4}$; 56 (paper)

This booklet is written with such an enormous frugality of words that, frankly, we have not been able quite to grasp the point—at least not firmly. One thing, however, seems clear; that at the present stage of the development of the author's theory it concerns the physicist more than it does the biologist.

LA CONNAISSANCE SCIENTIFIQUE.
By Général Vouillemin. *Albin Michel*
9 francs $4\frac{3}{8}$ x 7; 159 *Paris*

A philosophical and metaphysical discussion having for its purpose to show the limitations of the scientific method.